DIATOMS AS INDICATORS OF ESTUARINE PALAEOENVIRONMENTS

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by

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ABSTRACT

The increasing interest in the use of palaeoenvironmental indicators and in particular diatoms to reconstruct past changes in sea level has highlighted the need for a more precise methodology that (a) provides quantitative reconstructions, and (b) is applicable to a wide range of sedimentary environments.

Despite the widespread and increasing recent interest in the use of diatoms as indicators of estuarine palaeoenvironments and sea-level change, existing interpretative models, based on simple classification of taxa into freshwater, brackish or marine forms, provide only qualitative estimates of past conditions. Resulting palaeoenvironmental reconstructions are at best crude, offering some indication of past mean sea level height, and at worst erroneous, as they fail to consider the effect of post-mortem transport and other taphonomic processes.

This study aims to address these problems for the coast of Britain by developing a more robust quantitative method for using diatoms as indicators of estuarine palaeoenvironments and sea-level change. More specifically, it aims to develop a quantitative predictive model (transfer function) that relates diatom assemblage composition to salinity, habitat, depositional environment and tidal level around the coast of Britain. This is done through the collection and analysis of a training data set of diatom assemblages and environmental variables (salinity class, elevation, grain size, habitat type and sediment organic content) from 25 sites around the coast of Britain.

Qualitative and quantitative relationships within the diatom assemblages and between the diatom assemblages and coastal environmental variables are explored using TWINSPAN and canonical correspondence analysis respectively. The key environmental variables driving diatom assemblages in the intertidal environment are shown to be elevation, salinity and sediment particle size. Habitat type and site location also explain a significant amount of variation in the diatom data, suggesting regional differences in diatom assemblages not accounted for by geomorphological and sedimentological differences between sites.

The final transfer function for inferring normalised tidal height has a root mean squared error (RMSE) of 0.26, and a squared correlation (r^2) between observed and diatom-inferred normalised tidal height of 0.61. Corresponding error estimates under cross-validation by leave-one-out are 0.34 and 0.35 for $RMSE_{jack}$ and r_{jack}^2 respectively. The poor performance of the model in comparison to published regional transfer functions is concluded to be due to the merging of data from a large number of sites over a large geographical area. Such merging has apparently introduced a large amount of noise into the diatom / elevation relationship, and is probably related to the increased heterogeneity and interaction of sediment type and elevation, and to the observed regional overprint in the diatom assemblages.

Analogue matching to infer Sample habitats from the diatom data performs with a success rate of 59%. Further merging of the habitat types based on ecologically similarities increases the success rate to 82%.

The correct scale of trade off between coverage of palaeoenvironments, fossil diatom species and reduction of regionality in the modern training dataset is an issue that needs further research before this model may be applied to core material to assist in palaeoenvironmental reconstructions.

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CHAPTER ONE

INTRODUCTION

1.1 Reconstructing environmental change in the estuarine environment

Sea levels have changed dramatically in the past and since this discovery, centuries ago, it has remained a popular field of research, not least because of its implications for the past, current and future activities of humankind. Sea level research is carried out on various time-scales: long term geological investigations (10^6-10^9 years BP); medium term Quaternary investigations (10^3-10^6 years BP); and short term historical changes (10^{-1}-10^3 years BP) (Carter, 1988). In the geological sciences the understanding of sea-level changes is well developed, and timing and rates of rise and fall in sea levels can be identified in the rock record (Carter, 1992). The two main drivers of sea–level change are now known to be plate tectonics and climate change, the latter encompassing effects of isostasy and eustasy. In the recent past strategic, as opposed to fundamental (see Tooley, 1987), sea-level change research has been motivated by the search for minerals and especially hydrocarbons.

Recent developments in scientific investigative techniques such as improvements in radiometric dating, satellite remote sensing and increasingly powerful computers and numerical models, have, over the past few decades, enabled a rapid development of our understanding of both the *mechanisms* and *history* of sea-level change in many places around the globe (see Pirazzoli 1996). These developments, coupled with the current political interest in understanding the causes, mechanisms and effects of sea-level change, have led to numerous recent investigations into past coastal environmental change as the key to a better understanding of the likely impacts of current and future sea-level rise on coastal regions.

That coastal environmental change is indeed an important contemporary issue is borne out in the establishment, in 1992, of the large-scale, multidisciplinary project, the Land-Ocean Interaction Study (LOIS). LOIS was a 6-year (1992 - 1998) National Environmental Research Council (NERC) project involving over 360 scientists. The project had the following broad aim:

'To gain an understanding of, and an ability to predict, the nature of environmental change in the coastal zone'.

(NERC, 1994)

One of the components of the LOIS study was the Land-Ocean Evolution Perspective Study (LOEPS). The research presented in this thesis is a separate project from the LOEPS, but it was formulated to meet some of the challenges raised through the LOEPS work. The LOEPS collected a large set of sediment cores from the east coast of England for an investigation into the history of coastal environmental change within this study area (NERC, 1994). Detailed sea level histories were reconstructed, using palaeoenvironmental indicators such as diatoms (microscopic single-celled siliceous algae of the class *Bacillariophyta*; see Palmer and Abbott, 1986), ostracods (small crustaceans; see Van Harten, 1986) and foraminifera (single-celled testate marine organisms; see Scott & Medoli, 1978, 1986), along with the sediment record itself, for a number of key study sites on the east coast such as the Humber (Metcalfe *et al.*, 2000) and the Fenlands (Brew *et al.*, 2000).

The use of diatoms in this way has a long history due to their sensitivity to salinity changes. Palmer and Abbott (1986) mention a number of early sea level studies using diatoms with the earliest record of this approach detailed by Halden (1929). Since then they have been used in a wide range of coastal palaeoecological studies (e.g. Alhonen, 1971; Buzer 1981; Hemphill-Haley, 1995b, 1996; Horton 1997; Schrader, 1978; Vos and de Wolf 1993b; Zong 1998; Zong and Horton 1999). Diatoms preserved in estuarine and coastal sediments provide excellent indicators of past environments and sea level change for the following reasons:

- diatoms occupy aquatic environments both as plankton and as benthos, attached to various substrates (see Round, 1981) and are therefore abundant in coastal and estuarine environments;
- there are thousands of species of diatom, each with its own environmental niche that it occupies;
- they are very sensitive to changes in the physical and chemical environment, for example many species have specific salinity preferences and their rapid life cycle ensures a quick response to changing conditions;
- their robust silica test can be well preserved in the sediment, and these remains are easily recoverable, and

- identification is possible to a low level, based on morphological features of the frustules.

The increasing interest in the use of palaeoenvironmental indicators and, in particular, diatoms to reconstruct past changes in sea level has highlighted the need for a more precise and generally applicable method of quantifying diatom remains. Despite their widespread use and increasing recent interest, existing interpretative models, based on simple classification of taxa into freshwater, brackish or marine forms, provide only qualitative estimates of past conditions. Examples include Hustedt's (1957) halobian system and Simonsen's (1962) salinity tolerance classification. Resulting palaeoenvironmental reconstructions are at best crude, offering some indication of past mean sea level height, and at worst erroneous, as they fail to consider the effect of post-mortem transport and other taphonomic processes. Vos and de Wolf's system (1998, 193a, 1993b, 1994), which utilises ecological groupings of diatoms within estuarine sedimentary environments, does take taphonomic processes into account and attempts to eliminate allochthonous taxa using a list of diatom and non-diatom criteria. This is an improvement, but there is still the possibility of large errors in removing or retaining certain taxa from the reconstruction. This study aims to address these problems outlined above, for the coast of Britain.

Hitherto very few modern coastal diatom datasets have been published for Britain, and these from a limited number of sites; the largest modern dataset published to date covers six northern Britain sites (Zong and Horton, 1999), and Gehrels *et al.* (2001) covers three U.K. sites. There is therefore a need for a fuller modern dataset that covers a broader range of coastal sites in Britain, and a better understanding of environmental controls on diatom distribution. This research is designed to meet these needs.

1.2 Study aims and objectives

The main aim of this thesis is to provide a more rigorous basis for the use of diatoms as indicators of estuarine and coastal environments, in particular in relation to sea-level change, by developing a better understanding of the relationship between diatom distributions and environmental variables. More specifically, it aims to develop a quantitative predictive model that relates diatom assemblage composition to salinity, habitat and tidal level around the coast of Britain.

In achieving these aims, the objectives are as follows:

1. To create a training data-set of diatom assemblages and associated environmental information (habitat, salinity, elevation, grain size and sediment organic content) from a range of intertidal sites around the British coast
2. To generate a fuller set of modern diatom data for the British coast than has hitherto been developed.
3. To classify types of estuarine environments according to distinct diatom assemblages and determine the key chemical and physical parameters driving these assemblages.
4. To exploit recent statistical advances in quantitative diatom-based palaeolimnology (see below) by developing a quantitative predictive model (transfer function) to reconstruct environmental variables such as palaeo-tidal position, and depositional environment.

A key characteristic of the coast is that of high-energy environments. This project will focus on the estuarine environment in relation to sea-level change because estuaries are relatively sheltered coastal environments where clastic and biogenic sediment records accumulate, providing material for studying stratigraphic, and hence temporal, changes.

In reference to objective 3, the project will take advantage of recent developments in palaeolimnological techniques (see Birks, 1995; Charles *et al.*, 1994) and, in particular, the development and application of a quantitative predictive model or 'transfer function' which has been developed to relate individual species to water quality (e.g. Bennion, 1994; Bennion *et al.*, 1996; Hall and Smol, 1992). The most useful feature of these models is that they can translate *qualitative* diatom assemblage information into *quantitative* reconstructions of a particular environmental variable, e.g. total phosphorus (Bennion, 1994, 1996). The method involves the creation of a training data set (or calibration dataset) of modern surface-sediment diatom samples from a large number of sites (e.g., 30-40 or more). From this dataset diatom species optima and tolerance along an environmental gradient can be calculated. These optima can then used to infer past environmental conditions, e.g. salinity, using an appropriate calibration equation. This approach is described in detail in Birks (1995). This methodology is now standard in palaeolimnology, e.g. Charles and Smol (1994). The development of a transfer function using estuarine diatoms has already been achieved successfully: for salinity in the Thames estuary by Juggins (1992); for sedimentation rates and

altitude in the Tees estuary by Plater *et al.* (2000); and for palaeo-tidal levels for six sites in northern England and western Scotland by Zong and Horton (1999), thereby demonstrating that the technique can be used in the estuarine environment.

In this study the training set for the transfer function comprises a number of intertidal sites from around the coast of Britain. To ensure the development of as widely applicable a model as possible it is important that the training set covers the full range of intertidal environments likely to be found in the fossil record. These environments may be described and classified according to a number of criteria including, tidal range, estuary type, depositional environment, geographical spread, climate or major vegetation. Many of these variables are inter-related, so a matrix is used to select sites based on estuary type and tidal range. As long as a good geographical spread is obtained, this matrix will naturally include variation in other important environmental variables.

The method used to sample intertidal sediments is a very important aspect of data collection; because this project aims to improve reconstructions of past sea-level change it is the sub-fossil diatom assemblage that is of interest, rather than the transient living diatom community. A pilot study has been carried out, at Sailors Holme on the northern shores of the Wash, to assess the depth at which the sediment should be sampled, and which technique is most appropriate.

Along with the diatom assemblage samples environmental data is also collected and analysed; specifically, salinity, elevation, grain size, sediment organic content and habitat. Relationships between the diatom assemblages and these environmental variables are investigated using multivariate statistical methods and a predictive model created for habitat and elevation.

1.3 Summary of thesis structure

Chapter Two reviews the current literature on the estuarine environment and its development, factors affecting environmental change in this environment, and palaeoecological methods for reconstructing past coastal environmental change. Chapter Three details the criteria for selecting sampling sites and describes the relevant characteristics of each of the sites in the dataset. Chapter Four describes the field and laboratory methods, data analysis, and issues of

diatom taxonomy. Chapter Five describes the diatom-environment relationships through descriptive and cluster analysis. Chapter Six explores these relationships by testing their statistical significance and develops a predictive model, or transfer function, for habitats and elevation based on the diatom training dataset. The concluding discussion follows in Chapter Seven.

CHAPTER TWO

DIATOMS AND ESTUARINE PALAEOENVIRONMENTAL CHANGE

2.1 Introduction

This chapter gives an account of previous research on diatoms as indicators of environmental change in estuaries. The estuarine environment is defined and described with a focus on the nature of the British estuarine resource. This is followed by a description of the nature of coastal environmental change, drivers and effects. There then follows an account of the different methods that have been employed to reconstruct changes in the coastal environment, and in particular sea-level change. This leads on to a detailed analysis of the use of diatoms as coastal environmental change indicators and the need for a new, quantitative approach that is applicable over a wide geographical area.

2.2 The estuarine environment

The estuary, as opposed to more open-coast environments, is used as the coastal environment to provide interpretation of sea-level change because of the potential for high-resolution sedimentary sequences that are well suited for the preservation of both clastic and biogenic sediments (Kidson, 1986). Other coastal environments such as cliffs, beaches and rocky shores are highly dynamic environments and consequently not favourable to deposition and certainly not the preservation of depositional sequences.

2.2.1 Defining the estuary environment

Estuaries have been defined in a number of more or less specific ways. In the simplest of terms an estuary is an area where freshwater and seawater intersect. Whilst this definition may seem simple, it is, as pointed out by Caspers (1967) in his analysis of definitions,

something that causes some confusion depending on the point of view from which it is approached. Cameron and Pritchard (1963) offer the following, widely quoted, definition of an estuary.

'...A semi-enclosed coastal body of water which has a free connection with the open sea and in which seawater is measurably diluted with freshwater derived from land drainage'.

Other definitions can be offered based on geomorphological, tidal, hydrodynamic, salinity, and biological grounds. The upper limit of the estuary can be taken as either the highest point of salinity incursion or the limit of tidal influence. The latter will normally occur further inland as the effect of the tide on backing up the freshwater river flow extends further than the incursion of the saline tidal water. Although the upstream effect of the tide is minimal it, nevertheless, leads to changes in exposure on a small vertical scale. As exposure is an important variable under consideration here, the upper limit of the estuary will be understood as the limit of tidal influence and not the limit of saline incursion.

2.2.2 Orogeny

In geological terms estuaries are transient features of the landscape. Most are formed by the incursion of post-glacial rising seas into river mouths and basins of non-marine origin. Other processes involved in estuary development are tectonic subsidence, glacial processes and fluvial erosion (Carter, 1988). A more detailed description of estuarine orogeny can be found in Dyer (1973) and Russel (1967). Ultimately sea level (long-term changes right through to diurnal tide) is the key variable governing all aspects of estuarine development.

2.2.3 Estuary classification

The estuarine environment is typically a dynamic one, especially relative to lake environments where many diatom-based palaeoenvironmental reconstructions have been carried out to date. Estuaries can be classified using ecological, geomorphological, hydrodynamic and salinity/stratification criteria (Dyer, 1973). Most of the estuaries considered in this project are of the 'drowned river' or 'coastal plain' variety, as defined by Pritchard (1967). There is an extensive body of literature on the sedimentary (e.g. Carter, 1988; Dyer 1973, 1979; Mclusky *et al.*, 1990; Prentice, 1968), chemical (e.g. Cameron and Pritchard, 1963; Dyer, 1973, 1979;

Mclusky *et al.*, 1990 and Pritchard 1955), hydrodynamic (e.g. Hansen & Rattray, 1966 and Pritchard, 1967) and ecological (e.g. Adam, 1978; Beeftink, 1976; Carter, 1988; Chapman, 1941, 1976; Mclusky *et al.*, 1990; Patrick, 1967) aspects of the estuarine environments.

All of the various classification methods are valid for the purposes for which they were developed and have been applied in various types of studies of the estuarine environment. The classification adopted for this study is developed further in Chapter 3, Section 3.2.

2.2.4 Geomorphology

The main mechanisms responsible for the movement of sediments within estuaries are wave transport, tidal transport and estuarine circulation (Postma, 1980). The estuary is a relatively sheltered environment and is therefore dominated by the tide rather than wave energy. This creates conditions suitable for the deposition of sands and fine-grained sediment leading to the creation of sand flats and/or mud flats. This sedimentation is augmented by the presence of salts in estuarine water causing clay particles to flocculate and settle.

Although mudflats are typical of estuaries, ultimately the sediments that make up the intertidal environment depend on the source of this depositional material. For example, the Solway Firth is cited as an uncharacteristically sandy estuary due to the source sediment coming from sandstone and glacial material (Solway Firth Partnership, 1996). This is also true for many estuaries in Scotland due to the hard nature of the bedrock material.

Sediment sources include fluvial sediments from the margins, shores and subtidal regions of the estuary themselves, along-shore sediments and marine sediments (see Guilcher, 1967). The dominant source of sediment supply can change over time, hence changing the sediment characteristics of the estuary, as shown by Plater *et al.* (1999) for Romney Marsh, England. The shape of an estuary has a strong influence on sediment transport patterns but chemical processes also strongly influence the movement of fine sediments (Carter, 1988).

Assuming a mixed supply of sediment grain size, the greater the shelter in the estuary the finer the particle size deposited. In addition to this effect, tidal energy is dissipated over the intertidal flats, losing more and more energy as it approaches MHW; consequently it is common to find the finest sediments deposited at the highest intertidal zone (Dyer, 1994).

This vertical accretion leads to a fining upward sequence, with silts and clays at the surface, although this sequence is subject to local variation in sediment supply and sea level history. Proceeding down the vertical height of the intertidal depositional environment will usually, as a generalisation, lead from saltmarsh through mudflats to, sediment supply allowing, sandflats. The processes of sediment accumulation, erosion and distribution in the intertidal environment have been the subject of a great deal of research resulting is an extensive body of literature on the topic (e.g. Allen G.P *et al.*, 1980; Allen J. R.L, 1994; Cahoon *et al.*, 1996; Daborn *et al.*, 1993; Dyer, 1994; Grant *et al.*, 1997; Paterson *et al.*, 1990; Postma, 1980; Pringle, 1995; Rusnak, 1967; Stevenson *et al.*, 1988; Uncles and Stevens, 2000).

2.2.5 Saltmarsh development and vegetation zonation

A well-documented process termed 'biostabilisation' assists intertidal sediment accumulation. The phenomenon of biostabilisation has been described and analysed in detail, principally by Paterson (1989, 1995), Paterson *et al.* (1990), Underwood and Paterson (1993) and Underwood (1993) but also by Austen *et al.* (1999), Coles (1979) and Westall and Rince (1994). These studies have shown that diatoms exude a sticky substance of expolymers that form a mat over the intertidal mudflat increasing its shear strength and reducing erosion. This increased sediment stability enables pioneering intertidal vegetation to colonise the sediments; most commonly species of *Salicornia*, although species of *Spartina* are also frequent early colonisers. Once established, vegetation encourages sedimentation through a number of mechanisms described by Long & Mason (1983). The frictional drag caused by the presence of the plants further slows the flood and ebb tide reducing its ability to carry sediment and leading to increasing sedimentation. Stems and roots may trap and bind sediment and reduce erosion whilst the growth of the plants adds organic matter to the sediment. Finally, the presence of plants can deter filter-feeders that would otherwise rework the sediment making it more prone to erosion. Coles (1979) points out that it is generally accepted that vegetation helps sedimentation by trapping sediment around the plants. This is an oversimplification since, whilst Chapman (1960) has described how hummocks do build up around pioneer plants in predominantly sandy sediment, Kestner (1975) observes that in fine grained depositional environments it is not so much the plants that aid accretion but that they *prevent* erosion (Kestner 1975).

With continued sediment trapping and accretion the sediment surface gradually rises. This rise is accompanied by successional colonisation of saltmarsh flora, producing a distinctive vertical zonation of plant species that is described by many authors and from many sites around the world (e.g. Allen and Pye, 1992; Beeftink, 1976, 1977; Chapman, 1940, 1960; and Long & Mason, 1983). The floral zonation has been shown by many authors to relate to gradients of environmental stresses including salinity, tidal range and exposure (e.g. Beeftink, 1977; Gough and Grace, 1998; Jacobson and Jaconbson, 1989; Leeuw, 1989; Portnoy and Valiela, 1997; Warren, 1993). Long and Mason (1983) describes three major floral zones on a saltmarsh: the low marsh zone below MHWN, the middle marsh around MHW and the high marsh above MHW. Chapman (1960) develops a slightly more detailed classification of intertidal vegetation communities, some of which are mentioned below.

An early coloniser into the low marsh is commonly *Aster tripolium* forming Chapman's (1960) Asteretum in the low marsh. This may be gradually invaded by species such as *Puccinellia maritima*, *Limonium vulgare*, *Triglochin maritima*, and *Spergularia maritima*, in the development of middle marsh communities, Chapman's (1960) Late Asteretum. This accretion continues, accompanied by a change to higher marsh vegetation communities, until the marsh surface is only reached by the highest spring tides. This high surface is usually fully vegetated apart from drainage channels and isolated depressions and pans. Given time, the diversity of this high marsh will increase and is described by Chapman (1960) as the General Saltmarsh Community; a term commonly applied in the literature. General Saltmarsh Community species in Britain include *Aster tripolium, Puccinellia maritima, Limonium vulgare, Triglochin maritima, Spergularia maritima, Festuca rubra, Juncus spp., Plantago maritima, Agrostis stolonifera and Armeria maritima.* Where a natural transition to a terrestrial environment is still preserved, the fresher back of the marsh may be fringed with *Phragmites australis* beds or may develop into *Alder* carr. The shrubby *Halimione portulacoides* is frequently found along the banks of creeks within the saltmarsh, reflecting its preference for free draining soils. In time, as the marsh matures, *Halimione portulacoides* can spread out from creek banks to form almost uniform stands (Chapman's (1960) Halimionetum) in high, well drained marsh. Further up estuaries, where the freshwater river flow has a stronger influence, the intertidal sediments may be colonised entirely by *Phragmites australis* forming dense reed beds such as is found at Blacktoft Sands, at the confluence of the river Trent with the Humber estuary. *Phragmites australis* beds also occur in the lower estuary at and above MHWS where the salinity conditions are oligohaline,

although they may expand down into polyhaline environments on creek bank levees (Warren *et al.*, 2001).

The vegetation succession described above is a generalised picture, which, in reality, is often blurred by geographical variation in the distribution of many saltmarsh plants, as well a host of other local factors such as marsh width, gradient, sediment type, coastal protection works, grazing regime and localised variations in topography.

On the lowest intertidal flats, sometimes extending into the subtidal zone, *Zostera* beds are often found.

2.2.6 Creeks

Usually a network of creeks drains the intertidal area. In mature saltmarshes these creeks can be very large and deep. The creeks funnel the incoming tide and drain away the ebb tide with the pattern of a creek system looks similar to that of a freshwater stream network (Redfield, 1967). The crucial differences are that water flows in both directions in creeks and bank-full flow is *far* more common in creeks, but, like streams, creeks may experience headward erosion and may shift laterally. The depth of a creek is limited to a level close to lowest low water (French *et al.* 1995b).

As opposed to being a predominantly erosional feature developed by the action of the flooding and ebbing tides, most creeks are thought to develop contemporaneously with the process of vertical accretion that leads to the development of saltmarshes, as in the creek systems of the North Norfolk marshes described by French *et al.* (1995b). In the Barnstaple estuary, USA, Redfield (1967) observed that the saltmarsh developed along the margins of spits, sandflats and sand bars. The broad sound between advancing tongues of marshland became the site of future creeks; the marsh therefore builds up around the creeks as opposed to creeks eroding down into existing saltmarsh

Usually, then, the base of the creek is neither uniquely an erosional nor depositional surface in a marsh that is at equilibrium with current sea level. Where the intertidal area is still adjusting to a change in sea level, the creek bottom may be incising or accreting accordingly. Whichever the overall geomorphological tendency, creeks may experience headward erosion.

Diatom blooms may be seen on the creek bed depending on the type of sediment, which can range from fine muds to gravel, and stage of the tide.

2.2.7 Pans

Saltmarsh surfaces often contain pans, or pools. Higher and more mature marshes tend to have a greater density of pans (Pethick, 1974). Pans are a distinctive environment within the intertidal area that offers very changeable and hostile conditions only suited to the most robust and adaptable of species. The pans retain estuarine water left by the retreating tide, which may evaporate to produce a hypersaline environment that often dries out completely during the neap tide cycle. Conversely, pans can also be filled entirely with fresh rainwater.

Pans form through a number of different mechanisms. Yapp *et al.* (1917) categorise the formation processes of saltmarsh and these are summarised by French *et al.* (1995b) as follows:

- *Primary* pans: these are flat-bottomed and broadly circular in plan. They are thought to form as a direct consequence of the irregular plant colonisation of bare mud flat surfaces and may be drained by headward cutting creeks;
- *Secondary* pans: formed via a similar process on secondary marsh surfaces formed by slumping of vegetated blocks at the marsh edge;
- Long sinuous *channel* pans: formed through damming of small creeks by bank failures. These may be subsequently covered over by overhanging vegetation (especially *Halimione portulacoides*) to form subterranean 'pipes' (Steers 1977);
- *Residual* pans: remnant of older, partly in-filled pans.

Long and Mason (1983) note a precursor to pan development as being tidal litter and surface rot. The bar patches created could either clear the way for colonisation by new species or lead to the development of primary pans as described above (French *et al.*, 1995b). All these forms of pans can be seen around the coast of Britain.

2.2.8 The case of *Spartina anglica*

Spartina anglica, common cord grass, is a new species derived from *Spartina townsendii*, itself a hybrid of the native *Spartina maritima* (small cord grass) and naturalised American

species *Spartina alterniflora* (smooth cord grass) (Fitter *et al.*, 1984). It is a very invasive plant, rapidly colonising previously bare intertidal flats. This does help stabilise the flats and coastal protection is the reason the species was introduced to many coastal areas in Britain, although it is damaging in terms of nature conservation. *Spartina anglica* stands bring the anoxic layer in the sediment very close to the surface and reduce the variety and abundance of invertebrates that would have been present in the open tidal flats. Spread of this species also reduces the area of open feeding ground for wading birds; hence there are efforts in many places, such as Holy Island, to restrict or eradicate this hybrid species (Frid *et al.*, 1999).

2.2.9 Estuarine ecology

Living at the freshwater-marine interface produces a number of environmental stresses including exposure, salinity changes, temperature changes, sedimentation, erosion, and tidal emersion. To survive in this environment organisms require specific physiological and metabolic or behavioural adaptations (Carter, 1988). As a consequence of the hostility of the environment and its short existence geologically, few species have fully adapted to it. Yet, although diversity is low, productivity is high with estuaries being one of the most productive environments in the world; saltmarshes have a productivity of 700 – 1300 cm^{-2} yr^{-1}, as high if not higher than tropical rainforests (Carter, 1988).

Plants that have adapted to the estuarine environment are discussed in section 2.2.5, above. The few faunal species that have adapted to the estuarine environment can be present in huge numbers including the invertebrate *Corophium volutator*, the mollusc *Hydrobia ulva* and the polychaete worm *Arenicola marina*. Other common estuarine fauna include, the polychaete worm *Nereis diversicola*, the common shore crab *Carcinus maenas* and the common cockle *Cerastoderma edule*, plus many other shellfish and numerous migratory and juvenile fish. The microphytobenthos and microphytoplankton of estuaries, of which diatoms form a crucial and major part, are at the base of the food chain and are, as a result, critical to all higher life in this environment.

2.3 The British estuarine resource

The British estuarine resource, which covers 43% of the coastline, is comprehensively described in the Nature Conservancy Council's Estuaries Review by Davidson *et al.* (1991). In terms of salinity profiles most British estuaries are moderately stratified, or partially mixed and the vast majority of them are macrotidal (tidal range of over 4 m) with only 6 being microtidal (less than 2 m tidal range) estuaries, according to Davidson *et al.* (1991). The dominant morphological types are the coastal plain (or drowned river valley) and bar-built estuaries, although this masks a geographical variation in the dominant type such as fjords and fjards dominating in Scotland. Britain boasts a wide diversity of saltmarsh flora, which has led to a number of authors categorising the British saltmarshes in terms of the vegetation, e.g. Adam (1978), Beeftink (1976), and Chapman, (1941). A number of species find their northern limit at the Solway Firth and the Firth of Forth, including *Halimione portulacoides.*

Many British estuaries have a long tradition of grazing in the summer months by cattle and sheep. The various grazing regimes employed produce different floral modifications as a result of grazing pressure, selective grazing and an increased nutrient supply. The presence of livestock can lead to poached sediment where marshes are over-stocked.

From a human perspective the estuarine environment has a high value in economic, social, environmental and recreational terms. In Britain large populations live on or near the shores of estuaries, such as the Humber estuary (Humberside), the Tyne estuary (Tyneside) and the Mersey estuary (Merseyside) providing industrial and trading centres. They are also important breeding and nursery grounds for many fish and other organisms because of the relative shelter and productivity of this environment compared to the open sea (Carter, 1988). Estuaries are also important in terms of bird conservation for the huge number of nationally and internationally important populations of breeding and migratory wildfowl and waders they support. Along with estuaries acting as a sink for sediments and nutrients, they also act as a sink for pollutants. The industrial nature of a number of British estuaries combined with this characteristic has led to long-term pollution in some areas and many estuaries are also the end recipient of sewage and agricultural run-off.

The tidal nature of estuaries coupled with the low-lying fertile land has led, over the centauries, to vast areas of the intertidal being reclaimed for agriculture. Consequently long

stretches of many British estuaries are backed by flood defence embankments, or walls, which restrict the landward development of saltmarsh and cut short the succession to terrestrial communities. There are, however, still areas that are not defended and where the natural succession is still to be found including many areas of the northern shores of the Solway Firth.

2.3.1 The threat of sea-level rise to the British coastline

In recent years a great deal of interest has surrounded the climatic influence on sea-level change because of the threat of human-induced climate change. The various sea-level rise scenarios suggested would all have a significant impact on British estuaries. Globally, around 1500 million people live at, or near, sea level (Carter, 1992). Populations along the east coast of Britain, and other North Sea basin coastal areas, are included in these numbers. Despite continuing isostatic rebound in Scotland since the end of the last glaciation, *circa* 10,000 years ago, Britain's vast coastline in relation to its area potentially exposes a large proportion of the land area and population to the risk of increased flooding or complete inundation. Much of the low-lying coastline of Britain could be under threat from rising sea levels (see Carter, 1992; and Shennan, 1993 for further information and maps) including large areas of the Fenlands, East Anglia and land bordering the Severn estuary. Hence, the problem of sea-level rise has become one of national and international political concern. Understanding the causes and consequences of sea-level change is crucial to the understanding of the potential effects of sea-level change, due to human-induced climate change. Future changes cannot be predicted without a sound understanding of the mechanisms and effects of past sea-level changes.

2.4 Estuarine environmental change

There are a large number of environmental variables that can impact on estuary environments, causing changes in biological distributions and sediment properties. Sediment availability, sea level fluctuations and wave intensity exercise a strong control over changes in coastal form (Carter, 1988). Many modern impacts on estuarine biology and geomorphology are human-induces such as pollution and sea defence development and these are generally local in terms of their direct impacts. One of the most fundamental impacts leading to changes throughout the whole estuarine environment is that of sea-level change. Estuaries themselves are the result of isostatic and eustatic adjustment to changing sea levels since the end of the

last glaciation and their general character and development is therefore intricately linked to this mechanism. For this reason, this discussion of estuarine environmental change focuses on sea-level change, definitions, causes and consequences.

2.4.1 Sea-level change: definition and causal factors

On a global scale the undisturbed oceanic surface is termed the geoid. In reality mean ocean surfaces vary up to 180 m from the geoid (see Carter, 1988, 1992). In British waters sea level is measured against a local standard – that of the mean sea level at Newlyn, Cornwall from 1915 – 1921, known as Ordnance Datum Newlyn. Mean sea level from this record is given as zero and all sea level measurements around the coast of Britain are given in relation to this level. Mean sea level at a locality is measured as the average surface level over a period of time, e.g. a month.

Mean sea level varies from the mean tidal level. This is frequently due to shallow waters causing a distortion to the tidal wave and, as a result an asymmetrical tidal pattern with mean sea level occurring above or below mean tide-level. It is, however, mean tide level that is easier to ascertain (and predict from sedimentary and palaeoecological evidence) and therefore this is used in the construction of sea level curves, rather than mean sea level (Jardine, 1986). Studies of sea level change are not consistent in their definition of what constitutes sea level and hence sea-level change. The different tidal measurements that are commonly taken and predicted are listed in Table 2.1 and these abbreviations are used in subsequent chapters. Of these, MLWS, MHWS, MTL, and MHWN have all been used to represent 'sea level' in different studies (see Kidson 1986).

Relative sea level in any given locality can change due to a number of different factors. Sea-level changes are essentially a change in the height of the sea relative to the height of the land, or vice versa, or a combination of both. Sea-level change research usually expresses this height in terms of changes in mean tidal level relative to a standard mean height, e.g. Newlyn Datum or a sea level index point. The concept of sea level index points is described in Van de Plassche (1986) and summarised by Horton (1997) as being 'a datum that can be employed to show vertical movements of sea level when information about the geographical position, environment, indicative meaning, altitude and age are established'. The indicative meaning of an indicator is the height of original deposition (Van de Plassche, 1986). Recently much

effort has been spent on establishing sea level index points in various localities throughout Britain (e.g. Horton, 1997; Shennan *et al.,* 1995; and Zong and Tooley, 1996). These changes in the relative level of the sea and the land occur over a number of different time scales due to combinations of various different causal factors.

Table 2.1 Tidal levels within the intertidal zone

Tidal Level	Abbreviation
Highest Astronomical Tide	HAT
Mean High Water Spring	MHWS
Mean High Water	MHW
Mean High Water Neap	MHWN
Mean Tide Level	MTL
Mean Sea Level	MSL
Mean Low Water Neap	MLWN
Mean Low Water	MLW
Mean Low Water Spring	MLWS
Lowest Astronomical Tide	LAT

Numerous authors have described the general mechanisms for sea level change (e.g. Carter 1992; Fairbridge, 1980; Pirazzoli 1996) which can be summarised as deriving from two chief drivers: climate change and plate tectonics.

Fairbridge (1980) describes three types of sea level changes affecting the estuarine environment. These are:

1. The tidal component – daily fluctuations in tide.
2. The secular component – slower changes over periods of years e.g. eustatic, isostatic and tectonic causes.
3. The morpho-tectonic component – due to the nature of the bedrock and sediments within the estuary.

In the absence of the second and third types of sea level change, the coastal environment will establish an equilibrium in terms of geomorphology and ecology, intimately related to the

timing, magnitude (means and extremes) and energy of the tide. The estuarine environment may maintain a dynamic equilibrium, keeping pace with sea level changes due to the second and third factors, depending on the speed of change and other factors such as supply of sediment.

The simplest of sea level change scenarios would involve a straight forward rise or fall of the sea or land surface due to one of the following factors: tides, eustasy, isostasy, tectonics or morpho-tectonics. Accounts of the effects of coastal tectonics are given in Stewart and Vita-Finzi (1998). In reality these three factors of eustasy, isostasy and tectonics do not act in isolation, leaving a complicated sea-level change history in the sediments that can, at times be misleading. To clarify the terminology used in sea level history research Shennan (1980) proposes that the terms transgression and regression should only be used to describe lithostratigraphic changes and not to imply processes of sea level change. For example, Palmer and Abbott (1986) describe how a diatom-inferred fall in sea level may actually be due to the development of a barrier, leading to a freshening of the habitat behind. Shennan (1993) also defines positive and negative sea level 'tendencies'. These terms are described as referring to the influence of marine conditions with an apparent increase in influence being a positive tendency and an apparent decrease being a negative tendency. Confirmation of whether these tendencies do reflect actual sea-level changes requires a further level of analysis.

Climate change (caused by small variations in the earths orbit around the sun, its tilt and precession plus changes in oceanic circulation due to ice movements and tectonics) initiating a cycle of glacial and interglacial periods has been the primary cause of sea-level change throughout the Quaternary in Britain. The growth and decay of ice sheets removed and then released water from the hydrological cycle, resulting in fluctuations in ocean volume and causing sea levels to rise and fall (Tooley and Shennan, 1987). A summary of Holocene sea-level changes, i.e. since the end of the last glacial period in Britain, can be found in Long (2000).

As the climate has been changing throughout the Holocene so therefore has the sea level been changing throughout this period as the land and sea adjust to the amelioration of the climate and consequent retreat of the ice sheets. Eustatic sea levels rose, as a result of ice-sheet retreat from about –55 m at 11, 500 Cal yr BP reaching modern elevations circa 6000 years ago

(Tooley and Shennan, 1987). Since this time most of the sea-level change has been the result of isostatic adjustment e.g. through rebound in de-glaciated areas or associated subsidence in the forebuldge areas. The changes are much slower in pace now than earlier in the Holocene and are confined essentially to isostatic effects rather than eustatic effects (in terms of adjusting to the interglacial period but not considering more recent human-induced climate change). In particular, isostatic adjustment is ongoing in Scotland, which is still rebounding from the removal of the ice sheets. There is ample evidence for this isostatic uplift in the raised beach profiles found around the Scottish coast (see Kidson 1986) showing that isostatic adjustment has, on average been greater than eustatic sea-level rise. There has, however, been considerable debate over the nature of the Holocene sea-level change history described by Kidson (1986).

2.4.2.1 The development of the estuarine environment

Estuaries are numerous when sea level is rising and scarce when it falls (see Dyer, 1995). The main period of estuary drowning (i.e. river-mouth drowning leading to estuarine development) ceased around 6,000 BP (Fairbridge, 1980). Radiocarbon dating has been employed to investigate the timescale of saltmarsh development and this suggests that the present-day large expanse of tidal saltmarshes was found no earlier than ~ 4000 BP, coinciding with the reduction in sea level rise from 2.5 mm/yr to 1.0 mm/yr (Dyer, 1995). Before 4000 BP the rapid pace of eustatic sea-level rise prevented saltmarsh growth. Since the rate of Holocene sea-level rise slowed saltmarsh accretion has been able to keep pace with, and in some instances outstrip sea-level rise. Evolution of tidal flats during the Holocene transgression suggests that these environments are able to achieve sustained vertical growth when sea level is rising at rates of at least 1 to 2 mm/yr (Wells, 1995).

There are three main responses of marshes to sea level change: drown, remain stable or grow. Marshes may or may not keep pace with sea-level change depending on sediment supply (see Allen, 1995) and / or erosion rates as well as artificial factors such as the presence of sea defences. Many estuaries exhibit a cliff-like edge to the saltmarsh (such as the Solway Firth saltmarshes) that indicates a zone of erosion, usually around MHWN. Although an overall trend towards erosion or accretion may exist in an estuary, the highly dynamic nature of coastal environments can results in frequent reversals for varying periods of time. As a result,

accretion is not as continuous as in many lakes but palaeoecological, and other types of analysis, as well as dating, can help pick up hiatuses.

Coastal sediments provide a record that can yield information about the changing coastal environment. Where a chronology can be established for the sediment record, processes such as sea-level change can be dated and local and regional sea-level curves drawn up. Numerous methods have been developed to interpret changes in the coastal environment that relate to the process of sea level change. Palaeoecological studies of the sediment record can provide information on the nature of the coastal environment in addition to that gleaned from analysis of the sediments themselves. These methods are examined in the next section.

2.5 Reconstructing coastal environmental change

2.5.1 Methods of reconstructing sea-level changes

There are numerous methods that have been employed in sea level research to reconstruct sequences of coastal environmental change and, by implication, sea-level change. These methods have been reviewed by a number of authors including Pirazzoli (1996) and Plassche (1986). Pirazzoli (1996) describes a wide variety of coastal features, depositional, erosional and biogenic in origin, that have been used as indicators of past sea level stands, such as fossil barnacles, emerged or submerged wave-cut platforms, tidal notches, sea caves, fossil barnacle encrustations, fossil mangroves, fossil coral reefs and micro-atolls.

The sedimentary stratigraphy and tectonics alone can provide a good deal of information about the changing coastal environment as sediment-type changes between peats, sand, silt and clay deposits and the sediment record alone has often been used to interpret patterns of estuarine palaeoenvironmental change and infer past and future sea-level change (e.g. Chang and Choi, 2001; Devoy, 1982; Haslett *et al.*, 1998; Plater and Shennan, 1992; Shennan, 1986, 1989; Van Wijnen and Bakker, 2001). Furthermore, other coastal features such as barrier deposits (e.g. see Roep, 1986) and coral reefs (see Hopley, 1986) can be identified, assisting interpretation of other evidence. This type of analysis alone can only give qualitative relative sea-level change histories, although, when combined with dating, local and regional sea-level index points can be established.

In addition to the interpretation of the sediments record itself, fossil organisms preserved within the sediment record can give additional environmental information. There are numerous methods in use. A comprehensive review of many of these palaeoecological methods of sea level reconstruction is given in Plassche (1986) including botanical remains (Behre, 1986), shell middens (Martin *et al.*, 1986), marine molluscs (Peterson, 1986), foraminifera (Scott, 1986), ostracods (Van Harten, 1986), gastropods (Laborel, (1986) and diatoms (Palmer and Abbott, 1986). Some of the main palaeoecological indicators in use are considered below, before a more detailed consideration of diatoms as indicators of sea-level change.

2.5.2 Palaeoecological indicators

2.5.2.1 Pollen

Pollen is widely used in Quaternary studies and applied to the reconstruction of many variables including climate, trophic levels, salinity changes and human impacts (see Lowe and Walker, 1997; Roberts, 1998). Pollen has been used to assist studies of sea-level change, e.g. Dawson *et al.* (1998), Devoy (1982), Rochon and de Vernal (1998), Roe (1999) and Spencer *et al.* (1998), but pollen on its own has limitations in terms of quantitative reconstructions and the fact that the pollen is mainly terrestrial in source and terrestrial pollen may have been dispersed over very great distances. Pollen is usually used in coastal palaeoenvironmental change reconstructions in conjunction with other indicators, such as diatoms, as in Denys and Verbruggen (1998), Healy (1995), Jennings *et al.* (1998), Long *et al.* (1998), Shennan *et al.* (1995), Spencer *et al.* (1998), and Zong and Tooley (1996).

2.5.2.2 Plant macrofossils

Despite the widespread use of pollen as a palaeoenvironmental indicator, the use of plant macrofossils in Quaternary studies actually predates the use of pollen (Lowe and Walker, 1997). Despite this, the use of botanical macrofossils such as wood, fruits, buds, scales and seed, are limited in their utility and hence use, as they are only found in those sediment types that readily preserve them, essentially peats, although Behre (1986) describes other sources as being water-derived sediments and water-logged coastal archaeological excavation sites.

Where suitable sediments are to be found, indicators species can be used to interpret environmental factors such as salinity, proximity of groundwater, position relative to MHW and storm flood levels (see Behre, 1986). However, in this review paper Behre also points out that it is preferable to obtain enough remains to reconstruct the palaeocommunity as intertidal plant communities generally display a distinct succession along the tidal gradient responding primarily to the associated gradients of salinity and exposure. Consequently changes in the plant community composition give a clear indication of environmental changes, which may be related to sea-level change; for example Shaw and Ceman (1999) use macrofossils to interpret rates of saltmarsh aggradation in response to sea-level change.

The advantage of being able to use plant macrofossil remains over pollen is that macrofossils can frequently be identified below the genus level and do not tend to travel far compared to the wide dispersion of pollen. Botanical macrofossils can be a useful tool in intercalated peat and minerogenic deposits in indicating the degree of freshwater influence and sea-level tendency but their limitations in terms of preservation affects their application to sea-level studies. In sea-level studies they are perhaps best used to compliment the information obtained from microfossil analysis.

2.5.2.3 Ostracods

Ostracods are very small crustaceans generally around 0.5 - 1.0 mm, usually calcareous bivalves. Ostracods are useful in sea-level studies as indicators of depth of deposition with both density and diversity changing with depth. A discussion of their use as sea-level indicators can be found in Penny (1987) and Van Harten (1986), and Roe (1999) provides a recent example of their application to sea-level change studies from eastern Essex together with pollen and lithostratigraphic evidence. They have also been used to reconstruct palaeotemperatures of seas and hence by implication, climatic fluctuations, such as Wood's (1993) North Sea Pliocene palaeotemperature reconstruction based on shelf ostracods. Whilst temperature, and to a lesser degree the nature of sediments, do have an impact on the spatial distribution of ostracods (as also found by Kilenyi (1971) in the Thames estuary) the key environmental parameter affecting their distribution is salinity.

Calcite ostracod fossils date back to the Cambrian providing potentially long records for palaeoenvironmental reconstructions, but Van Harten (1986) gives the resolution of ostracod

tidal height reconstructions at the order of 10^2 m, although some species can provide a better resolution. Penny (1987) suggests that a resolution of 0.5 m to 1.0 m can be obtained in microtidal environments of the Kattegat. Ostracods may, therefore, offer greatest value in integrated multi-proxy palaeoenvironmental studies. Teaming ostracods with foraminifera is recommended by Penny (1987) as offering a more thorough and accurate tool. This particular combination of indicators is applied successfully to a brackish bay in Atlantic Canada by Tibert and Scott (1999) and to a Holocene sedimentary sequence in the Bohai Sea, China by Xue *et al.* (1995) whilst Mitlehner (1992) gives an example of using ostracods along with diatoms to reconstruct the palaeoenvironments of the Hoxnian Nar Valley Clay in Norfolk, England.

2.5.2.4 Molluscs

Molluscs are invertebrate animals which secrete a shell. The use of molluscs as sea-level indicators is reviewed by Petersen (1986). In this paper Petersen concludes that communities can be used in a qualitative manner, as indicator species, to distinguish between littoral, shallow- and deep-water environments, but that molluscan species 'cannot be assigned a high indicative value' in relation to sea-level change. Investigations into the dominant mollusc species in shell midden (artificial accumulations of shell fragments accumulating as an early human waste dump) have been used in Brazil to indicate the palaeoenvironment of the area surrounding the shell midden (see Martin *et al.*, 1986). Molluscs are less amenable to precise quantitative reconstructions in the way that foraminifera and diatoms are, because of problems of shell breakage (some issues of molluscan taphonomy are investigated by Martin *et al.* (1996) and Zenetos (1990)) and broader tolerances although there are examples or quantitative applications such as reconstructions of water depth by Norton (1967) and sea level by Petersen (1981), the latter with limited success. Hudson *et al.* (1995) discuss the use of molluscs as palaeosalinity indicators integrated with microplaktonic and microbenthic remains. As with ostracods, an integrated approach makes the best use of the molluscan record in palaeoenvironmental studies.

2.5.2.5 Foraminifera

Foraminifera are singled-celled marine organisms that secrete tests between 0.1 - 80 mm, of various robust materials. Foraminiferal assemblages are controlled by a variety of

environmental variables, not necessarily related to sea level, but the distribution of saltmarsh foraminifera is primarily controlled by elevation above mean sea level, as shown by Scott (1976). Their distribution also reflects the zonation and distribution of vascular plants (see Jennings and Nelson, 1992; Scott and Medoli 1978). These marsh species have narrowly defined vertical ranges, some less than 10 cm, thus making fossil marsh foraminifera useful indicators of intertidal palaeoenvironments and palaeotide levels (Scott & Medoli, 1978, 1986). Vertical ranges of marsh foraminiferal assemblages in relation to elevation above MHW have been described for many areas around the world such as Chezzetcook inlet, Nova Scotia and Tiajuana Lagoon, California (Scott & Medoli, 1978), Oregon tidal marshes (Jennings & Nelson, 1992) and UK intertidal environments (Horton *et al.*, 1999). Assemblage zones have also been used to infer palaeosealevels by numerous authors (e.g. Cearreta, 1998; Horton 1997, Jennings and Nelson, 1992, Jennings *et al.*, 1995; Scott *et al.*, 1996). More recently modern data sets of foraminiferal assemblages have been used in Britain by Horton (1997, 1999) to develop transfer functions to quantify sea-level changes. Taphonomic processes similar to those discussed in relation to diatoms in section 2.6.3 influence foraminiferal assemblages and recent research has begun to address the nature and impact of these processes on foraminiferal life and death assemblages (e.g. Barbieri, 2001; Cearreta and Murray, 2000).

2.6 Diatoms as indicators of estuarine palaeoenvironmental change

The above examples of palaeoenvironmental indicators offer a versatile toolkit to sea-level change researchers. Of all these indicators diatoms are as good as any and better than most in the qualities they offer for palaeoenvironmental change interpretation and are the most widely applied (Horton, 1997). Diatoms are microscopic single-celled algae that secrete two siliceous valves. They have a size range from 1 µm to more that 1000 µm, but most are in the size range 10-100 µm. Diatoms are from the class *Bacillariophyta* and live in all aquatic environments. More detailed information on the biology, morphology and general taxonomy of diatoms can be found in numerous texts including Darley (1977), Duke (1977), Patrick (1977), Round (1981), Round *et al.* (1990) and Werner (1977).

2.6.1. Life form and habitats

Diatoms can be split into two main life forms: planktonic and benthic. They can also be split morphologically into centric and pennate forms. Some exist as individuals whilst others grow together in chains or tubes. Food production is via photosynthesis. It is useful to divide the two broad categories of planktonic and benthic further based on habitat preferences.

Planktonic diatoms form an important part of the primary production in oceans and estuaries. In temperate estuaries it is common to find two main diatom blooming periods, in spring and autumn. These blooms are triggered by changes in temperature, light penetration and nutrient availability (Round, 1977). Planktonic taxa are frequently encountered in intertidal sediment samples as they are brought in and deposited on the tide and some species can occur in very high proportions, such as *Paralia sulcata* (although some debate exists about its exact life-form, see section 5.3.5). *Paralia sulcata* is a highly silicified species that forms long chains and the deposition of these chains on the intertidal sediments together with its resistance to dissolution accounts for its high abundance in some surface sediment samples. A high proportion of planktonic taxa are centric, although this is not exclusively the case.

Benthic diatoms can be split into a number of main habitat preferences:

- Epipsammon: species living attached to or between sand grains;
- Epipelon: species which live, unattached, on or in the sediment;
- Epilithon: species living on firm rock substrates;
- Epiphyton: species living attached to plants, either by gelatinous pads or stalks.

The epipelon are particularly important component of the estuarine diatom flora both in terms of their abundance and also the role they play in sediment stabilisation as a precursor to saltmarsh development (see section 2.2.5).

2.6.2 Environmental variables affecting estuarine diatom distribution

Diatom assemblages are the net result of a variety of factors effecting each species' abundance and distribution. These factors include salinity, pH, nutrients, temperature, tidal exposure, grain size, vegetation and predation. Human-induced water quality changes can also have a marked affect on diatom distribution, especially in heavily polluted estuaries. The exact

make-up of an assemblage changes as any one of these factors change, although some a stronger influence than others. Useful reviews of the ecology of intertidal diatoms and impact of these different environmental variables are given by Admiraal (1984), McIntire and Moore (1977), and Wilkinson (1980). The key environmental variables that affect the distribution of diatoms are discussed below.

2.6.2.1 Salinity

Salinity is a key environmental variable that diatoms respond to and is of paramount importance in interpreting sea-level change as, in general, a rise in sea level will lead to an increase in average salinity at any particular point (that was not already fully marine) within an estuary as conditions become more marine and, *vice versa*, a drop in sea level will see a drop in salinity. This change in salinity in turn leads to changes within the diatom community present, as the habitat in that area is altered. This relationship between diatom community composition and salinity has long been recognised, hence diatoms have been used as salinity indicators and by inference sea-level indicators (e.g. John and Pizzuto, 1995; Robinson, 1993). The main salinity gradient within an estuary is from the mouth to the head and Juggins (1992) records a strong gradient along the Thames estuary decreasing towards the tidal limit. At any point within an estuary the average open water salinity may follow such a pattern but at individual transects across the intertidal environment the situation can be very different. Underwood (1994) shows that salinity across the intertidal gradient is affected by other parameters, which include the phase of the tidal cycle and also the seasons.

In the estuarine environment the salinity regime is not constant and fluctuates daily, even hourly, with the movement of the tides. Diatoms adapted to the estuarine environment must be able to cope to some degree with these salinity fluctuations and hence it is more their adaptability rather than a salinity optimum that characterises true estuarine species (Snoeijs, 1999). Estuarine diatoms that do appear to have a salinity range preference may also be restricted by other environmental constraints on their distribution such as light, temperature, nutrients and degree of wave action (Snoeijs, 1999). Because of this inherent adaptability to changing salinity levels in diatoms common to the estuarine environment it makes little ecological sense to classify an individual species' salinity preferences beyond the broad categories of true fresh, oligohaline, mesohaline, polyhaline and euhaline (see section 4.5.2).

Snoeijs (1999) suggests that over 90% of diatom genera can actually be identified as simply having a marine or a freshwater affinity.

2.6.2.2 pH

Diatoms are sensitive to pH changes in the aquatic environment. The distinctive changes in diatom communities resulting from varying pH levels has led to their widespread use as indicators of acidification in upland lakes and streams (see Battarbee *et al.*, 1999; Smol *et al.*, Eds, 1986).

Through photosynthesis diatoms increase the pH of their surrounding environment but they also need to be able to withstand, to some degree, anaerobic conditions below the sediment surface, which creates a selective pressure on diatom species; the physiological adaptations required are not fully understood (Admiraal, 1984). Diatoms are classified into groups based on the pH preferences of alkalibiontic, alkaliphilous, indifferent, acidophilous and acidobiontic, although some debate exists over the utility of the indifferent class (Battarbee *et al.*, 1999).

2.6.2.3 Nutrients

Essential nutrients such as, phosphate and nitrate are rarely limiting in estuarine waters, although silica can be (Admiraal, 1984). Artificially elevated nutrient supply to estuaries from sewage discharges and agricultural run-off alters the diatom assemblages. The effect of increased nutrient supply to freshwater habitats on diatom community composition has been extensively studied (see Hall and Smol, 1999) but it is also known to have an impact on brackish diatom communities too (see Snoeijs, 1999).

The main impact changing nutrient levels have on diatoms is in term of a change in the relative proportions of nitrogen, phosphorus and silicate. Where sufficient silicate is available diatoms are usually superior competitors for nitrogen and phosphorus, but when silica becomes depleted and the N:Si and/or P:Si ratio decreases diatom growth can become limited (Tilman *et al.*, 1982). Different species of diatoms have different competitive abilities in terms of nutrient uptake, leading to changing in the diatom community composition as

nutrient ratios shift. Species of the *Stephanodiscus* genus are common indicators of elevated nutrient levels.

Eutrophication in the Black Sea has been shown to have a dramatic effect on the diatom community with its dominance in terms of primary production being replaced by dinoflagellates and other non-siliceous flagellates (Vasiliu, 1996). This shift from pelagic primary production away from diatoms in favour of non-siliceous flagellates is due to a reduction in silica caused by eutrophication (see Snoeijs, 1999).

As with pH, the diatom community response to changing nutrient levels (in particular phosphorus) has been widely used to reconstruct nutrient enrichment histories in inland water bodies (see Hall and Smol, 1999).

2.6.2.4 Temperature

Intertidal benthic diatoms exhibit a high tolerance to fluctuations in temperature (Admiraal and Peltier, 1980), which occur on a daily basis with the changing tides. Despite this tolerance, some epipelic species common on intertidal flats disappear in the summer months and this has been linked to increased temperature (Colijn and Dijkema, 1981) revealing that temperature does exert a selective pressure on intertidal diatom communities.

Over the period of the Quaternary temperature has fluctuated greatly, and these far larger fluctuations in temperature, compared to daily and seasonal change at present, can be picked up in the diatom record assisting in the elucidation of the history of climate change. For example, diatoms extracted from marine sediment cores from the eastern Antarctic margin have been used to assist in reconstructions of climate change, along with the occurrence of ice sheets in the area (Taylor and McMinn, 2001). *Paralia sulcata* has been shown to be temperature dependent (see Zong, 1997); autecological knowledge such as this for species that are frequently abundant in the diatom record is of significant use in interpreting the indicative meaning of a fossil assemblage.

2.6.2.5 Exposure

Exposure due to the tidal nature of estuaries is a key variable controlling the distribution of diatom species and hence the composition of diatom assemblages. Exposure times can be calculated with knowledge of the tidal regime (e.g. Gehrels, 2000). Exposure is the ecological variable that the diatoms are responding to rather than elevation (Nelson and Kashima, 1993). Many intertidal epipelic forms rely on a degree of exposure as it is in this period of time that they photosynthesis. Increasing levels of exposure leads to an increase in desiccation thus giving the competitive advantage to aerophilous diatoms such as *Navicula cincta*. As exposure is directly, and for the majority of the intertidal gradient roughly linearly (see Gehrels, 2000) related to height, most authors use elevation as a proxy for the ecological variable of exposure. This approach has been used successfully by a number of authors including McIntire (1978), Nelson and Kashima (1993), Oppenheim (1988), and Zong and Horton (1998) to suggest a strong relationship between diatom distribution and elevation (hence exposure).

Many pennate epipelic species are motile. This locomotive ability allows these species to retreat into the sediment as the tide comes in and return to the surface as the tide goes out, in order to photosynthesise. Paterson *et al.* (1986) develop a technique for preserving the fine vertical distribution of diatoms within the top few millimetres of the intertidal sediments for analysis using low temperature scanning electron microscopy. This technique is employed by Paterson (1986) in a study of the migratory behaviour of estuarine epipelic diatoms. Paterson (1986) concludes that light is the controlling factor for the onset of diatom migration to the surface and that different diatoms have different thresholds triggering this movement, the first to appear on the sediment surface being *Navicula* and *Nitzschia* species. Such species would not be adapted to living in the subtidal zone due to the lack of exposure (Underwood, 1994) and hence they are specifically adapted to life in the intertidal zone.

2.6.2.6 Grain size

Diatom species also show a preference for different substrates with some species uniquely adapted to soft, silty sediment surfaces and others adapted to the more mobile sands (the epipelon and epipsammon respectively). Studies of diatom assemblage composition from intertidal habitats have shown the composition to change markedly with changing substrate

characteristics (e.g. Amspoker, 1978; De Jonge, 1985; Nelson and Kashima, 1993; Risnyk, 1973; Wilkinson, 1976; Zong and Horton, 1998). The relationship of diatom subfossil assemblages to sediment properties of grain size is explored in detail in the following chapters.

2.6.2.7 Light and turbidity

Turbidity cuts down light penetration and can smother and block habitats. Estuaries are characteristically turbid environments due to the high sediment loads, so most diatoms encountered in estuaries will be able to tolerate a certain degree of turbidity. But levels of turbidity may exercise some selective pressure. For example *Paralia sulcata* has been shown to be prefer conditions of low light (Conover, 1956).

Snoeijs (1999) discusses a modern light-related phenomenon presenting recent evidence for compositional changes in Baltic Sea planktonic diatom communities, thought to be caused by increased UV radiation due to ozone layer depletion.

2.6.2.8 Vegetation

Epiphytic diatom species, such as many *Achnanthes* and *Cocconeis* species may show preferences for particular plant species. In terms of the saltmarsh flora, although diatom assemblage distribution may show a close correlation with the higher plant vertical zonation, this does not indicate a causal relationship but rather, is reflecting the fact that both diatoms and higher plant distributions are controlled by the same major intertidal environmental variables of salinity, substrate and exposure. Subtidal epiphytic forms such as *Cocconeis scutellum* can be found in high abundances on the intertidal environment, presumably due to tidal redistribution (see section 6.3.4).

Saltmarsh vegetation can have a direct affect in diatom community composition through shading of the substrate reducing light penetration, but also retaining moisture (Oppenheim, 1988).

2.6.2.9 Predation

Diatoms form the primary food source of a large number of molluscs such as *Hydrobia ulva* as well as zooplankton, invertebrates and other infauna. Some predators exhibit a selective preference for certain diatoms, which can alter the composition of the diatom assemblage.

The living diatom assemblage at any one time is the net result of all the above pressures. Therefore, a cautious approach should be adopted when interpreting low or high abundances of an individual species to ensure that this are not put down to changes in one environmental variable, where a combination of factors may be the cause (Snoeijs, 1999).

2.6.3 Post-depositional changes

The list of variables discussed above act on the composition of the living diatom assemblage. There are, however, post-depositional taphonomic processes at work leading to the loss of autochthonous valves and the introduction of allochthonous valves, which can have a significant affect on the structure of the death assemblage (Simonsen, 1967). These taphonomic processes include: selective dissolution; corrosion; fragmentation; transportation through re-suspension, sediment re-distribution and erosion; and bioturbation. A number of these processes have been investigated in order to provide firmer grounds for distinguishing between autochthonous and allochthonous species in a death assemblage.

The full suit of taphonomic processes affecting sub-recent intertidal diatoms is investigated and discussed in relation to diatoms from St Catherines Island, Georgia, by Sherrod *et al.* (1989) revealing significant differences between life and sub-recent assemblages and implications for palaeoenvironmental reconstruction are discussed.

Numerous experiments have been carried out on diatom dissolution including: Flower (1993), who found no relationship between age and extent of preservation in an investigation of aspects of diatom preservation and breakage in relation to the character of the depositional sediment; and Mikkelsen (1980) who found some relationship between dissolution and valve morphology and a close relationship between degree of fragmentation and degree of dissolution in a diatom assemblage. Further information on dissolution can be found in Bradbury (1973), Johnson (1974), and Kamatani and Riley (1979). Other taphonomic

processes have received less attention. The issue of transportation is addressed by Beyns and Denys (1982), Ferrante (1977), and Huettal (2000). Fragmentation is also addressed by Beyns and Denys (1982) and Flower (1993).

2.6.4 Advantages of diatoms as palaeoenvironmental indicators

The range of benefits attached to diatoms as indicators of palaeoenvironmental change include the following:

- They are abundant and diverse;
- They are cosmopolitan in distribution;
- Their high diversity (estimate range between 10,000 to 100,000 species world-wide) and niche requirements means they are very sensitive to changes in their environment and their rapid life-cycle ensures a quick response;
- Their silica cell wall means that they preserve well in sediments, they are relatively easy to prepare from sediment, and they are suitable for study using conventional light microscopy;
- They are amenable to quantitative reconstructions as one valve represents half an individual diatom cell.

Alongside the advantages of using diatoms as environmental indicators, there are also disadvantages. Learning diatom taxonomy takes time and there is continual debate over correct classification and nomenclature of numerous species. In turn, this is exacerbated by the fragmented nature of the literature and the tendency for different taxonomic schools to lump together or split species and genera. For many species their autecology is poorly known. In the estuarine environment taphonomic processes, such as post-mortem transport (leading to the loss of autochthonous species from the record and the addition of allochthonous species to the record), dissolution, breakage and post-depositional re-suspension lead to significant differences between the living community and the death assemblages (Sherrod, 1989; Simonsen, 1967). However, this is not a problem restricted to diatoms, but one common to most fossil bio-indicators in the estuarine environment, including foraminifera and molluscs (see Martin *et al.*, 1996). Research into taphonomic processes and the development of

'taphonomic grades' (e.g. Martin *et al.*, 1996) are helping to address this problem for many palaeoenvironmental indicators.

Nonetheless these problems are not insurmountable and do not out-weight the numerous benefits of using diatoms in coastal palaeoenvironmental studies and they remain one of the most reliable and versatile indicators providing detailed results.

2.6.5 Qualitative methods of interpreting the estuarine diatom record

Following recognition of the important role salinity plays in diatom distributions, various salinity sensitivity classification systems have been developed (e.g. Hustedt, 1957; Simonsen, 1962; Schrader and Schuette, 1981; Van de Wulf and Huls, 1957) and Palmer and Abbott (1986) summarises these schemes, bar Van de Wulf and Huls (1957), as follows:

1. Polyhalobian (marine: greater than 30 parts per thousand salinity)
2. Mesohalobian (brackish water: 2-30 parts per thousand salinity)
3. Oligohalobian (fresh water: less than 2 parts per thousand salinity and subdivided into 'halophilic' and 'indifferent' classes)
4. Halophobes (true freshwater forms, intolerant of any salt)

To this summary can be added a fifth class of 'euryhaline' taxa, which are taxa with a very broad salinity tolerance from marine to freshwater.

These classification systems only provide qualitative estimates of past conditions and then only of salinity, therefore allowing rather crude interpretations of sea level and related estuarine environmental changes. Furthermore, Palmer and Abbott (1986) draw attention to the fact that these systems are limited in their use by taxonomic and reliable habitat data whilst their application, often concentrating on indicator species rather than whole assemblages, may fail to consider taphonomic processes such as post-mortem transport (see Sherrod *et al.*, 1989) which can all mean that, at worst, results and interpretations are quite erroneous.

More recently, Vos and de Wolf (1988, 1993a) developed the idea of assigning salinity tolerances to look at salinity preference and life form of diatoms found in specific estuarine

depositional environment. On this basis they developed a classification system for diatoms specifically relating to the estuarine environment, first published in 1988 and modified in 1993a. This system classifies macrotidal, mesotidal and non-tidal sedimentary environments according to the relative abundance of 14 diatom ecological groups ranging from marine plankton to freshwater plankton. These ecological groups are based on salinity preference and life form. This system offers a greater degree of precision in environmental reconstructions in estuaries compared to the above methods, and also provides helpful criteria for distinguishing between the autochthonous and allochthonous component of an assemblage. The technique has been utilised in sea-level change research by Metcalfe *et al.* (2000), Shennan *et al.* (1995a; 1995; 1996a; 1996b) and Zong and Tooley (1996). It still, however, remains qualitative and cannot be used to convey quantitative environmental information for more detailed palaeoenvironmental reconstructions in the estuarine environment. Furthermore, the wide ranges of abundance possible for various ecological groups make application ambiguous, and results and their interpretation uncertain. Moreover, whilst Vos and de Wolf apply their system with a reasonable amount of success to case studies in the Netherlands (Vos and de Wolf, 1993b, 1994) where the system was developed, it is questionable just how applicable the system would be when extrapolated to estuarine systems elsewhere.

2.6.6 Examples of diatoms as indicators of coastal environmental change

From the preceding discussion of diatom ecology it can be seen that diatoms are highly sensitive to coastal environmental changes related to sea-level change, such as changes in salinity and exposure. Diatoms have therefore been used in a wide variety of past sea level and coastal environmental change studies over a range of time scales. Some examples of these applications are given below.

A combination of isostatic uplift and eustatic sea-level rise led to a complicated series of transgressions and regressions in the Baltic Sea during the Holocene. Evidence is seen in the landscape through a vertical series of palaeo-shorelines with associated archaeological remains. Alhonen (1971) utilise the local diatom record combined with C^{14} dating from a series of isolated lake basins to assist the interpretation of the sedimentary record to provide a sea-level curve for the area.

Shennan *et al.* (1996) also analysed the diatom record (along with other biological remains) from an isolation basin, the Ardtoe isolation basin, NE Scotland to reveal raised and submerged shorelines and rivers. There are many other examples of the qualitative use of diatoms to assist in the interpretation of past sea-level change, and to validate sea-level index points (e.g. Dawson *et al.*, 1998; Healey, 1995; Metcalfe *et al.* 2000; Robinson, 1993; Shennan *et al.*, 1995a, 1995b, 1996a, 1996b; Spencer *et al.*, 1998; Zong and Tooley, 1996). Some studies have gone on to ascertain diatom communities indicative of altitudinal zones relative to tidal levels (e.g. Dawson *et al.*, 1998; Hemphill-Haley 1995a; 1995b; 1996; Nelson and Kashima, 1993; Shennan *et al.*, 1995; Zong, 1997b; Zong and Horton, 1998), which can provide a more detailed approach to reconstructing sea-level changes. Denys and de Wolf (1999) and Cooper (1999) provide recent reviews of the utility and application of diatoms as indicators of coastal and estuarine palaeoenvironments and relative sea-level change.

To move to a more applied field, diatoms have also been used to establish the presence of land bridges that could have been important for human movement such as the Bering Straits land bridge between Russia and Alaska, whose closure date is still disputed. Josenhans *et al.* (1997) used diatoms to help reveal the existence of other land bridges between, what is now, the off shore Queen Charlotte Islands and the U.S.A. mainland around Washington. Diatoms from sub-aerial basins, marine cores, palaeoshores and drowned rivers were used and categorised into fresh, brackish and marine communities. This diatom data helped establish the presence of a land bridge between 13,500 and 9500 (C^{14}) years BP, therefore making part of the North West USA coast accessible and habitable during this time. As well as human migration route and times of movement, this sort of work can yield useful information about ocean circulation (between Pacific and Atlantic), which in turn helps in the understanding of past climatic changes. A review of further applied estuarine studies aided by diatoms can be found in Sullivan (1999).

The preceding examples all examine to a greater of lesser extent quite gradual changes, but there are also quite abrupt episodes of coastal environmental change, either permanent of temporary, that are also recorded in the sediment and hence diatom record.

The sedimentary and diatom record in the Washington and Oregon coastline been studied by a number of authors including, Hemphill-Haley (1995a, 1996), Hutchinson *et al.* (1997, 2000) and Shennan *et al.* (1996) to produce records of tsunamis and accordingly earthquakes in the

Cascadia subduction zone over the last 3000 years. Intertidal marsh and lagoon sediments, characteristically slack-water muds and peats, may contain continuous beds of coarser material laid down during floods, windstorms, storm surges or tsunamis. These sediments will generally contain microfossils. Hemphill-Haley (1995a, 1996) used diatom stratigraphy from just such environments to identify the source of the coarser material and therefore confirm that the band in question was a marine incursion caused by a tsunami. Hutchinson *et al.* (1997, 2000) employ diatom analysis of lake sediments from the emerging coast of Vancouver Island to identify recurring tsunami run-up deposits in this same subduction zone. Storm-surge deposits in Britain have also been identified in the coastal record with the aid of diatom analysis from Romney Marsh (Plater *et al.*, 1999) and from Morecambe Bay (Zong and Tooley, 1999).

Estuaries can also be a very good source of archaeological remains and complimentary biostratigraphic investigations can assist archaeologists by providing information on the palaeoenvironmental conditions that the archaeological finds are found in and hence assist their understanding of the archaeologically inferred human activities. The use of diatoms in archaeology is reviewed by Battarbee (1988) and more recently by Juggins and Cameron (1999). The Thames has quite a history of this type of study. Rapid tectonic subsidence of the London Basin and southeast England led to the belief that the Thames was a freshwater river as far south as Crossness during Roman times, whilst at present it is tidal to 30km above the city of London (Battarbee, 1982). Diatoms were used by Battarbee (1982) to confirm that the Thames was tidal as far as Pudding Lane during the Roman occupation. This was achieved by analysing diatoms from deposits taken in front of a series of revetments dating back over 2000 years; the deposits in front of the quay constructed around AD 70 displayed a characteristic estuarine assemblage, not freshwater. This discovery has important implications for the functioning of the port that was constructed around this time.

These above examples of the use of diatoms in the study of estuarine palaeoenvironmental change prove them to be a versatile and useful tool. The studies mentioned so far all rely on diatom assemblage evidence in a more or less qualitative manner with diatoms being taken as indicative of zones along an environmental gradient, such as low salinity or circa MHWS. However, diatoms can also be used to develop quantitative predictive models for reconstructing changes in environmental variables and this approach is discussed below.

2.6.7 Quantitative methods of interpreting the estuarine diatom record

Recent advances in diatom palaeolimnology have provided a methodology for quantitative reconstructions of estuarine environmental change. Theses advances involve using the diatom record to develop a transfer function for the reconstruction of nutrient levels (e.g. Bennion, 1994; Bennion *et al.*, 1996; Charles and Smol, 1994; Fritz *et al.*, 1991; Hall and Smol, 1992) and pH levels (Birks *et.. al.*, 1990; Dixit *et al.*, 1991; 1993; Korsman and Birks, 1996). These reconstructions are interpreted as records of eutrophication and acidification respectively.

The development of a transfer function involves two-stages of statistical analysis:

1. Regression: the relationship between species and the one or more environmental parameter is modelled using a training data set.
2. Calibration: the model is applied to fossil data, transforming qualitative species data into quantitative palaeoenvironmental reconstructions.

This approach makes use of the fact that diatom assemblage composition is more sensitive to changes in environmental variables, such as pH or altitude, than the broad categories often used in simple classification schemes (described in the sections 2.6.2 and 2.6.5 above). It also utilises the fact that diatom distributions tend to follow a continuum of change along an environmental gradient, rather than abrupt zones, as shown by McIntire (1978) and Sullivan (1982). Diatoms do not, therefore occur as discrete assemblages, except where there are abrupt changes in the gradient, e.g. at a saltmarsh cliff (Sherrod, 1999). To make use of this sensitivity more detailed ecological information is needed in order to model accurately the relationship between species data and environmental variables. The collection of an adequate training set of diatom assemblages and modern environmental information covering a high proportion of palaeoenvironments and fossil species is therefore crucial to this technique.

Juggins (1992) provides the first example of this approach in an estuarine environment. Quantitative relationships between modem diatom assemblages in the Thames estuary were modelled in order to develop a transfer function for reconstructing palaeosalinity. The results revealed a gradual extension of the tidal head up-river over the last 2000 years. Since this work a number of other authors have developed local estuarine diatom-environment transfer functions. These include a model for reconstructing palaeotide levels developed from six British estuaries by Horton (1997) and Zong and Horton (1999), which has also been applied

to the reconstruction of sedimentation rates and altitude in the Tees estuary by Plater *et al.* (2000). Gehrels *et al.* (2001) developed a diatom transfer function from three U.K sites, as well as a variety of combinations of multi-proxy approaches using diatoms, testate amoeba and live and dead foraminifera. This study concluded that 'the accuracy and precision gained [through the multi-proxy approach] may be disproportionate to the amount of time invested in analyses additional to that of diatoms', suggesting that diatoms are the single most useful microfossil to use in developing a sea-level change transfer function. Sherrod (1999) also developed a diatom-based transfer function from Puget Sound, Washington to reconstruct salinity and elevation. These examples demonstrate that the technique can be used successfully in the estuarine environment. Horton (1997) has also applied the technique to formainiferal assemblages to reconstruct past sea-levels for the North Norfolk coast and Gehrels (2000) also applied the technique successfully to foraminiferal assemblages from the coast of Maine, USA. As yet, no attempt has been made to develop a detailed quantitative diatom-environment model for application to estuaries over a much wider geographical area in Britain.

Recently there has been some debate over the correct geographical scale at which to develop and apply a coastal microfossil transfer function for the purposes of reconstructing local sea-level change. This debate stems from the publication of a number of studies applying local microfossil transfer functions (e.g. Gehrels, 2000; Gehrels at el., 2001) and regional microfossil transfer functions (e.g. Edwards and Horton, 2000; Plater *et al.*, 2000; Zong and Horton, 1999), with varying degrees of success. The debate centres around the potential noise introduced into a larger (in terms of geographical coverage of sites) training dataset and the effect this may have on the predictive ability of the resultant model when applied to a local reconstruction.

The argument in favour of a local model is that it avoids merging data from a variety of sites with variances in environmental factors such as tidal regime, sediment supply, timing of flood and ebb tides and flooding frequency. However, although a locally derived transfer function theoretically, by minimising noise, maximises the predictive ability of the resultant model, it also minimises its utility in terms of the breadth of its predictive ability.

The potential benefit of a larger training dataset is that it increases the number of diatom species in the model, as well as the variety of estuarine environmental conditions. This

reduces the number of likely no-analogue situations encountered when applying the predictive model to fossil diatom assemblages. Not only does it reduce the number of fossil diatom species with no analogue in the predictive model training dataset, but it also increases the diversity of estuarine environments that this model can be used to predict, hence covering more of the palaeoenvironments that are potentially encountered in the fossil record. However, the more samples from different sites are added to the training dataset the more this has the potential to increase the noise in the dataset and hence decrease the predictive ability of the resultant model.

Even using a transfer function derived from 6 northern British sites, Plater *et al.* (2000) concluded that the relatively poor results in some areas of the palaeoenvironmental reconstruction stemmed from the lack of equivalent representative environments and associated diatom assemblages in the training dataset. Therefore, although the potential for increasing noise must be taken into account, there is still a need to develop larger geographical scale training data sets, that, as concluded by Gehrels *et al.* (2001), ' increase the likelihood that environmental information from modern training sets accurately reflect palaeoenvironmental conditions'.

CHAPTER THREE

SITE SELECTION AND DESCRIPTION

3.1 Introduction

This chapter describes the procedures used to select the 26 intertidal estuarine sites to be used for the collection of modern estuarine diatom samples and appropriate accompanying physical, chemical and biological data. Each of the 26 sites are described in turn, in terms of their topography, geomorphology and ecology.

3.2 Site selection

Two hundred potential sites were identified from a map-based survey working from the full list of estuaries in Britain identified and classified by Davidson *et al.* (1991). This list had to be reduced to a manageable number of sites that were possible to sample within the timeframe of the project whilst yielding a sufficient variety of intertidal environments to construct the transfer function. Of these 100 sites, 75 were visited to assess suitability and those that could not be visited were assessed using available literature. Sites were rejected on the grounds of inaccessibility for fieldwork, and accepted according to the type/variety of intertidal habitats present at the site. This process reduced the number of sites to 50.

In selecting a final set of sites for inclusion in this study it was important to ensure that the full range of intertidal environments potentially present in the fossil record were sampled, given that modern analogues could be found. Estuaries have been classified according to numerous other environmental parameters (see section 2.2.3). Davidson *et al.* (1991), in the NCC Estuaries Review of Great Britain, devised a classification of estuaries integrating Fairbridge's (1980) 5 categories of estuary, based on morphology and origin, with three additional categories of their own, also based on morphology and origin. The classification adopted by Davidson *et al.* (1991) is combined with tidal range in this study to draw up a matrix of estuary type that will include the majority of estuarine environments. This system is adopted

because of its simplicity, suitability and geographical coverage of application in the NCC Estuaries Review. Many of the other variables by which estuaries are categorized in the literature are inter-related. Therefore, as long as a good geographical spread is obtained along with a variety of morphological types and tidal ranges, the set will naturally include variation in other important environmental variables. These tidal and morphological categories are shown in Table 3.1.

Table 3.1 Tidal range classification after Davies (1993) and Hayes (1975)

Range (Average spring tidal range)	**Classification**
< 2 m	Microtidal
2 – 4 m	Mesotidal
> 4 m	Macrotidal

Each estuary was then assessed for suitability for inclusion in the final survey. Initially, estuaries were selected to ensure a sampling site was chosen from all the classes in the matrix in Table 3.2, apart from those that are rarely, if ever, found in Britain. These are essentially the microtidal environments, with the exception of bar-built estuaries. Estuaries were then added to the set sequentially to increase the geographical spread of sites within the study area. Within this selection criteria described, each individual site was assessed for inclusion according to the following attributes:

- Variety of intertidal habitats present;
- Naturalness/lack of pollution;
- Accessibility;
- Safety; in some intertidal environments, access across the saltmarsh for sampling purposes involves crossing very large creeks that it is either not possible to cross or that would involve the danger of being cut off by the incoming tide. Very broad intertidal environments also come with the risk that sampling and surveying cannot be carried out without a similar risk with the incoming tide. Another safety aspect is the soft unconsolidated nature of many intertidal mudflats rendering them difficult and dangerous to cross on foot.

The southwest coast of Scotland (Dumfries and Galloway) was chosen as a northwestern limit of selected estuaries. This is because the Solway coast is well documented as being both the north-western and south-western limit of numerous species of coastal and intertidal flora and fauna such as *Halimione portulacoides*, natterjack toads and the honeycomb worm *Sabellaria alveolata* (Solway Firth Partnership, 1996). This site therefore forms a natural north-western limit to this study in terms of homogeneity of flora and fauna. Furthermore, Scottish firths and estuaries further north from the Solway are generally quite different geomorphologically reflecting the bedrock material that provides the source material for the intertidal deposits, again setting them apart from the otherwise more homogenous set.

Holy Island, in northeast England, forms the north-eastern limit of the sites as, according to the description and mapping of maritime vegetation communities in Rodwell (2000) a number of key communities find their north-eastern limit around Holy Island, including *Salicornia* saltmarsh and *Spartina anglica* saltmarsh.

Three minor alterations were made to the categories used by Davidson *et al.* (1991) in the final matrix of estuaries shown in Table 3.2. These are: the amalgamation of the fjord and fjard category; the omission of the rias category; and the omission of the linear shore category used by Davidson *et al.* (1991). The latter two are omitted simply because there are very few of these estuary types around the coast of Britain and, once the above selection process had been completed none of these estuaries were selected for the final set of sites. This does not effect the integrity of the final set of sites because rias are similar in character to coastal plain estuaries and the barrier beach sites selected on the North Norfolk coast also bear many similarities to linear shore estuarine deposits. Fjords and fjards are amalgamated into one, partly due to similarities of geomorphological type, but also because most of these are beyond the northern limit of this study so differentiating between these two types is less important. The only sites that falls into this category are the fjards of Skyreburn Bay and the Cree Estuary (Wigtown site).

Table 3.2 Matrix of final selection of estuaries

Estuary Type ⇒ ---------- Tidal Range ⇓	Fjords and Fjards	Coastal Plain	Bar-Built	Complex	Barrier Beach	Embayment
Microtidal < 2 m	N/A	N/A	Poole Harbour	N/A	N/A	N/A
Mesotidal 2 - 4 m		Lymington Deben	Alnmouth		North Norfolk Coast (2 sites)	Hamford Water
Macrotidal > 4 m	Cree Water of Fleet	Blackwater Severn (3 sites) Humber (4 sites)	Exe	Solway Firth (2 sites)	Holy Island	Bridgewater Bay Wash (3 sites)

Some mesotidal estuaries and one microtidal estuary are included in the set for variety and completeness, but the majority of the sites are macrotidal. This reflects the fact that over two thirds of British estuaries are macrotidal (Davidson *et al.* 1991). In addition, macrotidal estuaries tend to have a more defined ecological continuum, which can be resolved into more distinct zonation. The only mesotidal complex estuaries within the geographical study limits are the Tyne and the Wear. Both of these were rejected on the grounds of restricted intertidal environments and contemporary pollution levels. There were also no mesotidal fjords or fjards within the geographical limits of the study area.

The ideal sampling site would cover the full tidal range, including the natural transitional environments from intertidal, through HAT, to supratidal. In reality there are very few intertidal sites left in Britain that have not undergone some form of truncation of the tidal range through the development of sea embankments or walls etc, either for the purpose of

flood defence or to reclaim and drain land, mainly for agriculture. Such sites do not present a complete environmental gradient up to HAT. The presence of embankments or sea walls interrupting the tidal gradient can lead to erosion at the foot of the artificial structure and, where a creek cuts into the high marsh and even reaches the foot of the artificial structure, flooding of the back of the marsh can occur earlier during the flood tide cycle than would otherwise be the case at that elevation. As diatom distributions respond to the duration of flooding, i.e. exposure (see section 2.6.2.5), this could have a modifying effect on the assemblage at the back of the marsh. In general, therefore, although the majority of sites do have some form of artificial embankment at the top of the site, the choice of transect location and Sampling Site location along that transect were made carefully to avoid such artificial modification as much as possible.

Some estuaries have more than one Sampling Site within them. These are indicated in Table 3.2. The final list of all 26 sites, within the 15 estuaries selected, is shown in Table 3.3; this table also indicates the existence and type of artificial truncation to the intertidal gradient. The geographical of distribution of the Sites is shown in Figure 3.1.

3.3 Individual sites description

For the purposes of the Site descriptions the Sites are ordered geographically, starting at Holy Island in North East England, and moving clockwise around the British mainland (see Table 3.3). For each estuary a general description is given of the geology, geomorphology, evolution, flora and fauna and human influences on the site. A description of the specific site(s) sampled within the estuary follows the general description of the wider estuary.

Some estuaries have more than one Sampling Site within them. In order to provide consistency in terminology, from here on the term 'estuary' is used to refer to the wider estuary and the term 'Site' is reserved for the actual sampling transects within an estuary. The precise terminology used is presented in Table 3.4. National gird references are included in Table 3.3.

Table 3.3. Table of Sites ordered geographically, starting with Holy Island and continuing clockwise around the coast of the British mainland

Site	Abbreviation	Region	Tidal Regime	Classification	Grid Reference	Embankment or sea wall?
Holy Island	HI	North East	Macrotidal	Barrier Beach	NU 09 42	None
Alnmouth	AM	North East	Mesotidal	Bar-Built	NU 24 10	Sea wall
Spurn Point	SP	Humber	Macrotidal	Coastal Plain	TA 40 11	Embankment
Spurn Saltmarsh	SM	Humber	Macrotidal	Coastal Plain	TA 41 14	Embankment
Welwick	WK	Humber	Macrotidal	Coastal Plain	TA 34 18	Embankment
Blacktoft Sands	BK	Humber	Macrotidal	Coastal Plain	SE 86 22	Embankment
Gibraltar Point	GP	Wash	Macrotidal	Embayment	TF 55 57	None
Sailor's Home	SH	Wash	Macrotidal	Embayment	TF 44 48	Embankment
Frampton	FR	Wash	Macrotidal	Embayment	TF 36 38	Embankment
Burnham	BU	North Norfolk Coast	Mesotidal	Barrier Beach	TF 81 46	Embankment
Stiffkey	SK	North Norfolk Coast	Mesotidal	Barrier Beach	TF 96 44	Embankment
Deben	DB	Southern East Anglia	Mesotidal	Coastal Plain	TM 28 45	Embankment
Hamford Water	HW	Southern East Anglia	Mesotidal	Embayment	TM 21 23	Embankment
Blackwater	BW	Southern East Anglia	Macrotidal	Coastal Plain	TL 87 05	Embankment
Lymington	LY	South Coast	Mesotidal	Coastal Plain	SZ 36 95	None
Poole Harbour	PH	South Coast	Microtidal	Bar-Built	SY 97 92	None
Exe	EX	South Coast	Macrotidal	Bar-Built	SX 99 82	Sea wall
Bridgewater Bay	BB	Severn	Macrotidal	Embayment	ST 25 45	Gabbion-basket defense
Wentlooge	WL	Severn	Macrotidal	Coastal Plain	ST 26 79	Embankment
Aust	AU	Severn	Macrotidal	Coastal Plain	ST 56 88	None
Arlingham	AR	Severn	Macrotidal	Coastal Plain	SO 69 10	None
Mawddach	MW	Wales	Macrotidal	Bar-Built	SH 61 14	Embankment
Bowness	BS	Solway	Macrotidal	Complex	NY 20 61	Embankment
Caerlaverock	CK	Solway	Macrotidal	Complex	NY 01 65	None
Skyreburn Bay	SB	Solway	Macrotidal	Fjard	NX 57 54	Embankment
Wigtown	WT	Solway	Macrotidal	Fjard	NX 44 56	Embankment

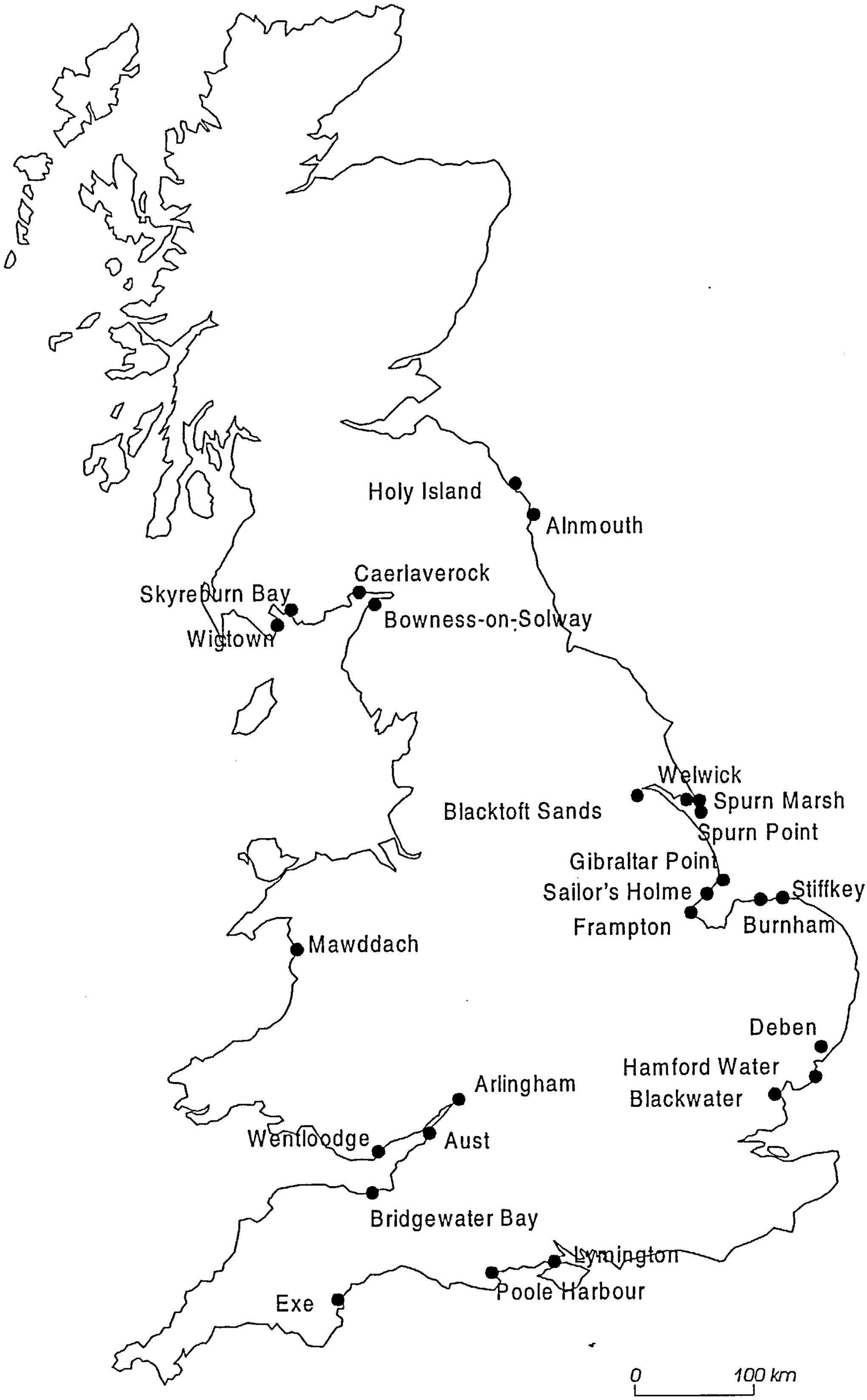


Figure 3.1 Map showing the location of the 26 sampling sites

Table 3.4 Sampling Terminology

Term	Abbreviation	Description
Estuary	Estuary	The wider estuary within which the sampling site was located
Sampling Site	Site	The site of the transect
Sampling Point	Point	Individual sampling points along the transect from where cores of sub-surface sediment samples were collected
Sample	Sample	An individual section of the cores taken at each Sampling Point

3.3.1 Holy Island

Holy Island, or Lindisfarne, is a small low-lying island off the coast of Northumberland, forming part of the set of islands known collectively as the Farne islands. It is a tidal island, the north-western end forming a tombolo. The island is accessible from the mainland for a few hours either side of low tide via a metalled causeway at the narrowest point between island and mainland.

The bedrock is Carboniferous Limestone (Visean) and the island is a continuation of the middle limestone formations of north-east England. Over the island, the Carboniferous strata tilt gently to the east consisting of sandstones, gannister, shales and limestone, (Galliers 1970). The island only became separated from the mainland during post-glacial sea-level rise in the Holocene and the outline of the island has changed very little over the past 400 years. There is also a volcanic sill intrusion forming the outcrop on the south side of the island, on which sits the castle.

Currently the island is square in shape with a narrow neck extending westwards towards the mainland, expanding into a round area - the Snook - at its western end. This western end is where the causeway from the mainland meets the island. This Snook and Snook Neck are covered in sand dunes.

The low, flat intertidal area in between the island and the mainland is classified as a macrotidal barrier beach estuary by Davidson *et al.* (1991). This area is approximately 1.5 km wide. The area drains through a network of small channels to a main channel in the south. Large areas of intertidal muds and sands are exposed at low-tide, providing rich feeding for many hundreds of visiting and resident wildfowl and waders.

There are a number of conservation designations covering the area. These include Lindisfarne National Nature Reserve, Berwickshire and Northumberland Shore candidate Special Area of Conservation, Lindisfarne Special Protection Area and Holy Islands Sensitive Marine Area. There is also the under-pinning SSSI designation.

3.3.1.1 Sampling Site: Holy Island (HI)

The location chosen for sampling was near the causeway, at the north-western tip of the island. Samples were taken along a transect on the island side of the bay. This side was chosen to ensure that samples were taken well away from the area on the west side, near the causeway, currently under disturbance due to an experiment to assess mechanical methods of *Spartina anglica* eradication from the area (Frid *et al.*, 1999).

The intertidal flats at the site near the causeway are mainly muddy sand and sand flats. The mud content increases nearer the marsh, but the sand content remains high. Low hummocks and 'spurs' of saltmarsh invade into the intertidal mudflats, vegetated mostly by low *Puccinellia maritima* and other saltmarsh grasses but with some *Salicornia* spp. and *Spartina* spp. too. These latter two pioneer species diminish in abundance rapidly up the tidal gradient giving way to a fully grass-dominant sward, which increases in height in a landward direction along with an appearance of occasional small shrubs of *Halimione portulacoides.* A zone with occasional low residual pans marks the transition to the high marsh community. The high marsh vegetation although baring similarities to Chapman's (1960) general saltmarsh community is somewhat lower in floral diversity with *Puccinellia maritima, Agrostis stolonifera* and *Armeria maritima* dominant species. The narrow road from the causeway to the island's village separates the marsh from the sand dunes beyond.

3.3.2 The Aln Estuary

The mesotidal bar-built Aln estuary and catchment is situated along the north-easterly edge of the Northumberland-Solway basin; a low-lying basin of sedimentary carboniferous strata across the north of England. The origin of this basin's complex structure lies in the closure of the Iapetus Ocean caused by the collision of the Laurentian and Avalonican continents through the late Sillurian and early Devonian. This Carboniferous sequence within the basin is made up of alternating layers of deposits of shallow marine coastal and fluviodeltaic origin (Chadwick *et al.*, 1995).

The river Aln in Northumberland drains the granite hills of the Cheviots and the northern limit of the Carboniferous sedimentary basin called the Northumberland basin. With the exception of the market town of Alnwick, 9 km upstream from the estuary mouth, the estuary drains a sparsely populated agricultural catchment, into the North Sea. The catchment area is 640 km^2 (NRA, 1996). The small coastal town of Alnmouth sits on the northern side of the Aln estuary.

As with many other stretches of the Northumberland coast, an extensive dunefield has developed, through the Holocene, at Alnmouth. This formation is described in detail by Orford *et al.* (2000) and Wilson *et al.* (2001). In summary, the solid geology in the catchment is overlain by Devensian glacigenic material. This material has been eroded by the Holocene transgressive shoreline and has also been carried down as alluvium to the coast by the river Aln. This sediment forms the bulk of the beaches and dunes now present (Orford *et al.*, 2000). The swash-aligned dunefield north and south of the Aln estuary mouth has formed on top of barrier beach deposits. These dunes are most extensive to the south of the estuary. It is this system that has created the bar-built estuary of the river Aln, providing shelter for the accumulation of fine sand, muds and organic matter.

On the northern shore of the estuary, flood defence walls restrict natural development of the estuary and result in a narrowed strip of saltmarsh in comparison to the southern shore of the estuary. On the southern side of the estuary some of the intertidal environment has been drained to create agricultural fields. At low tide the waters in the channel of the estuary are shallow enough to walk across between the north and south shores.

3.3.2.1 Sampling Site: Alnmouth (AM)

The location chosen for sampling was on the northern side of the estuary. Although the intertidal area is much less extensive on this shore of the estuary, there is clearer habitat zonation as well as a wider variety of habitats. The sediment is sandy, with some areas of silt deposition in the most protected locations, such as at the foot of the sea walls. The high saltmarsh at Alnmouth is dominated by *Halimione portulacoides*. There is also a clear pioneer zone of *Salicornia* pp. *Spartina* spp. is wide-spread within the estuary, in places forming large monoculture stands. In these areas the trapped sediment is noticeably finer than elsewhere in the intertidal zone. *Arenicola marina* casts are common throughout the sandflats, and in creeks and pools within the saltmarsh.

3.3.3 The Humber

The Humber estuary, on the East coast of England, is one of the largest estuaries in the country. Aspects of the evolution of the Humber and current status have been intensively studied including its Holocene evolution, geomorphology, sediment movements, water quality and pollutant movements, ecology, and sea-level change history (e.g. Al-Bakri, 1986; Barr *et al.*, 1990; Hardisty and Rose, 1996; Long *et al.*, 1998; Metcalfe *et al.*, 2000; Pethick, 1993). More recently the estuary has formed the main site at the core of LOEPS investigations (see Shennan and Andrews, 2000). It is therefore important that sites from this estuary are included in the training data set as it is a key site where a more quantitative approach to reconstructing sea-level change is needed to compliment and enhance existing and ongoing research.

The Humber is a macrotidal coastal plain estuary that drains 25% of the area of England. There are a number of river estuaries nested within it; these are the rivers Hull, Derwent, Ouse, Aire, Don, Trent, and Ancholme. Of these the Ouse is by far the largest catchment, itself comprising a number of other river systems. The Humber drains a total catchment area of 24,000 km^2. The Holocene evolution of the estuary is described by Long *et al.* (1998) and Metcalfe *et al.* (2000). The narrow Humber Gap that cuts through the chalk escarpment that forms the Yorkshire and Lincolnshire Wolds divides the broader outer estuary and narrow inner estuary (Long *et al.*, 1998). Sandstones and marls make up the bedrock geology in the west, with limestone and Cretaceous chalk in the east.

Human influence on, and modification of, the estuary has been marked over the centuries. From Mediaeval times onwards, extensive wetland drainage was carried out on the Humber wetlands. The Humber is fringed with flood embankments cutting off the natural succession of intertidal environments that occur in the geological record for the area. In addition to this geomorphological and consequential floral modification of the estuary, the Humber and its shores have been, and continue to be, heavily used for fishing, ports and shipping, as a location for industry and, in some areas, for recreation. All these pressures have affected the water quality of the Humber, although it is now improving (Hardisty and Rose, 1996).

Despite extensive land reclamation flood embankment development, the Humber still contains large areas of saltmarsh such as Welwick saltmarsh in the outer estuary. In the inner estuary where salinities are lower, *Phragmites australis* beds can be found. There is a net surplus of sediment in the estuary (Long *et al.*, 1998) and extensive intertidal flats and subtidal sandbanks in the outer estuary.

3.3.3.1 Sampling Site: Blacktoft Sands (BK)

The area encompasses numerous artificial lagoons (made to attract wading birds and wildfowl), and some of the most extensive *Phragmites australis* beds in the country. Blacktoft Sands reserve runs for 3 - 4 km along the convergence of the rivers Ouse and Trent to form the Humber estuary. A flood embankment running around the back of the beds restricts their extension inland, whilst a training wall, built in the 1930's to trap silt and maintain the shipping channels, has allowed the *Phragmites australis* to spread across the resultant mudfalt. Only high spring tides of spring and autumn flood the *Phragmites australis*, and the track behind them. The site is an RSPB owned and managed nature reserve, and an SSSI.

The area of the reserve chosen for sampling was across the narrowest stretch of the *Phragmites australis*. This runs west to east out from the flood embankment to the river Trent. The reed bed was largely impenetrable, partly due to the height (up to 9 feet) and density of the reeds, but also because of the network of large, soft muddy creeks running through the reeds. At the seaward edge of the reeds, the gradient increased quite steeply down towards the training wall and reeds are replaced by *Scirpus maritimus* (sea club-rush). In

some areas, the rush zone extended down to a high training wall, but more usually they grade out to leave a strip of bare, soft mud between the rushes and the wall. At one point the reeds stop abruptly next to an actively accreting wide area of mudflat, behind the training wall. There are no transitional vegetation zones in this area. The sediment here is very soft, deep silt.

Beneath the reeds near the river the sediment surface was very smooth, silty and quite dry. At the back of the reed bed, nearer the embankment, the sediment was wetter and more peaty in comparison.

3.3.3.2 Sampling Site: Welwick Marsh (WK)

Welwick saltmarsh is on the northern shore of the Humber estuary at the western end of the area sheltered by the Spurn.

The area is known to be accreting at present (English Nature staff, pers. comm.), due to its sheltered location in the lee of the Spurn peninsula, an area known as Spurn Bight. Welwick saltmarsh is a large square of saltmarsh in a sheltered corner formed by a dog-leg in the sea wall at the point where Partrington channel drains into the Humber. The saltmarsh tapers along the coast to the east. The bedrock in the locality is Cretaceous chalk, overlain by clays and alluvium.

The gradient of the saltmarsh is quite gentle and smooth reflecting the relatively low wave energy at this point in the Humber. It is drained by a system of deep creeks. The saltmarsh also displays good vegetation zonation unmodified by grazing or any other human-induced floral or geomorphological changes.

A flood embankment built in 1900 forms the back of the saltmarsh. At the foot of the embankment the ground is very water-logged and is dominated by *Spartina*. This strip is only three to four metres wide. Beyond this there is a wide, flat high saltmarsh of Chapman's (1960) general saltmarsh community moving into a zone dominated by *Puccinellia maritima* and *Aster tripolium*. As the gradient begins to steepen a ridge and creek system begins to develop. *Halimione portulacoides* appears on the ridges, with *Spartina* dominating the creeks.

The low saltmarsh is dominated by *Puccinellia maritima.* As the saltmarsh level continues to drop *Spartina* begins to increase in dominance, and creeks and ridges increase in density. The transition to mudflat is quite abrupt at a very low cliff with some small peninsulas of saltmarsh extending into the flats. *Spartina* spp. and low densities of *Salicornia* spp. also occurs in small, well-defined islands near the boundary of the saltmarsh. There area a number of shallow primary pans in the mudflat but these peter out within a few meters of the saltmarsh. The mudflat then extends 3 to 4 kilometres out to the low-tide channel of the Humber.

Spartina anglica was planted in the 1930s, 1940s and 1960s to the east of Welwick. This has led to its continuing spread along the edge of Welwick saltmarsh.

3.3.3.3 Sampling Site: Spurn Marsh (SM)

Spurn is a naturally occurring spit that has developed at the mouth of the Humber as a result of long-shore drift from the Holderness coast to the north. The Spurn has periodically been breached, or washed away to lesser or greater extent throughout recorded history. Researchers are undecided as to whether, left to nature, the Spurn would experience a cyclical existence or whether it would be gradually migrating west, with waves washing over periodically removing sand from the east side and depositing it on the west side. What *is* known is that sea defences have held the feature in an unnatural position for some time now, and erosion now threatened to destroy the peninsular as it has not been able to adjust in response to natural geomorphological and hydrological processes.

Extensive mudflats have developed in the shelter of this peninsular with a narrow strip of saltmarsh connecting to the Spurn. The Spurn itself is host to plant species typical of mobile sandy habitats such as Marram grass and sea holly. Spurn is a National Nature Reserve and SSSI owned by the Yorkshire Wildlife Trust. Permission for sampling was given by the Trust and English Nature.

This Spurn Marsh site is located at the narrow neck of the peninsular. An embankment protects the Spurn from the west, and a grassy bank, on quite a steep gradient, drops down to the high saltmarsh. The flat high saltmarsh is dominated by *Halimione portulacoides.* Tops

of creeks then begin to appear and the creeks widen as the saltmarsh surface gradually drops in height. The creeks all run roughly perpendicular to the embankment. These creeks are numerous and soon develop into a parallel creek and ridge system. Vegetation becomes a little more mixed before giving way to almost bare sediment ridges with occasional patches of *Spartina anglica*. The surface of the ridges appear to be undergoing erosion. This is evident through the firm, mammallated surface as opposed to the soft, smooth surface of actively accreting silty sediments. Continuing down the intertidal gradient *Spartina* increases in patch size, density and abundance but peters out as the low saltmarsh gives way to bare mudflat.

Although the height of the ridges begins to decrease, the parallel ridge and creek effect continues for some distance out into the mudflat, albeit much reduced in relief. The soft mud surface in the creeks is about 2 cm deep, and on the ridges it is 4 cm or more. Below the soft, recently deposited sediment there is a consolidated clay layer. A similar environment is described from the Wash by Coles (1979), who concludes that this is a characteristic of an environment undergoing accretion. 500 metres out onto the mudflats there are still distinct higher, drier surfaces, divided by slightly lower creeks running perpendicular to the coast.

3.3.3.4 Sampling Site: Spurn Point (SP)

This site is out at the head of the Spurn (see description above), and is named Spurn Point. The energy of the environment here is too high for the finer sediments to build up, as they have further inland along the lee of spit. Instead, wide sandflats have built up in the lee of Spurn Point. A high sea wall at the back of the sandflats protects the terrestrial land of Spurn Head. The sand is quite coarse, and there is much evidence of shellfish and other infauna such as *Arenicola maritima*.

3.3.4 The Wash

The Wash is a large, shallow macrotidal embayment on the east coast of Britain. It drains an area of roughly 12,900 km^2 including the catchments of the rivers Steeping, Witham, Welland, Nene and Great Ouse. The drainage area is of low relief. It has a maximum depth of over 30 metres in the Lynns Deep channel at the mouth of the embayment. The intertidal area comprises 45% of the total area of the Wash (Davidson *et al.* 1991) with low tide exposing broad intertidal sand and mudflats. The Wash also has the largest area of saltmarsh

in the UK (Burd, 1989). Altogether the area is of very high conservation importance, especially as a feeding ground for birds. Consequently it is designated an SSSI, Ramsar site and SPA.

The Wash is all that is left now of a far more extensive tidal basin in Jurassic and Cretaceous rocks (Evans, 1965). The rest of the basin has been filled in by Quaternary deposits of peats and muds forming the Fenlands (Wilmot and Collins, 1981). Holocene deposits associated with rising sea levels are also found in the Wash. The last phase of deposition of silt in the Wash began just before Roman times and is still on going (Evans 1965), although the rate is declining, possibly due to reduced sediment supply (Pye 1995). Accretion dominates in the intertidal, and erosion dominated in the subtidal with tidal processes dominating throughout the Wash (Pye, 1995).

Despite the large drainage area, the rivers entering the Wash do not supply any appreciable amount of sediment to the Wash because their low gradients restrict their ability to transport sediment. Wilmot and Collins (1981) quantified the fluvial sediment supply to the Wash and confirmed that fluvial sediment supply to the Wash is several orders of magnitude less than the amount of sediment known to be carried in suspension over the intertidal flats of the Wash annually. Hence, the net flux of sediment movement is seaward to landward (Collins *et al.* 1981). The bulk of the depositional material in the Wash is thought to come from a combination of the floors of the Wash and the adjacent areas of the North Sea, plus the eroding boulder-clay cliffs of Lincolnshire, Holderness and northeast Norfolk (Evans, 1965).

Evans (1965) identifies six intertidal depositional environments in the Wash as being: the saltmarsh; higher mudflats; inner sandflats; *Arenicola* [*marina*] sandflats; lower mudflats; and lower sandflats. Evans (1965) suggests that these sequential depositional environments build up on top of the next most seaward environment in a 'sheet-like unit'. A seventh environment is identified cutting across all of the above - creeks and bordering areas. In some areas the saltmarshes are not accreting but eroding and where this is the case where sandflats border with the saltmarsh rather than mudflats, as in the depositional sequence above (Coles, 1979). These distinct environments still hold as an accurate description of the Wash today.

The intertidal environment of the Wash has been greatly manipulated by human activities, which in turn has altered natural geomorphological processes. Land has been reclaimed for

agricultural use by the building of artificial embankments since Roman times (Evans, 1965). Coastal engineering works, including land reclamation have led to increased accretion in front of these structures in many areas around the Wash (Inglis and Kestner, 1958).

3.3.4.1 Sampling Site: Gibraltar Point (GP)

Gibraltar Point is an SSSI and a National Nature Reserve (NNR) managed by the Lincolnshire Trust for Nature Conservation. The Reserve acts as a sanctuary for nesting shorebirds in the spring.

The sampled site is an area of high saltmarsh cut through by the Steeping river just before it enters the Wash through a channel known as Wainfleet Harbour. At this point the Steeping river is strongly influenced by the tide, and is a small estuary nested within the wider embayment of the Wash.

The vegetation is dominated by *Halimione portulacoides* to the extent of appearing to the eye as a continuous monoculture carpet of this shrubby species. However, the back of the saltmarsh is vegetated by a grassy sward (*Puccinellia maritima*) with abundant *Hydrobia ulvae*. The commencement of the *Halimione portulacoides* zone is marked by the landward extent of the creeks through the saltmarsh consistent with the fact that *Halimione portulacoides* is adapted to a well-drained soil (see section 2.2.5). Some creeks peter out up the saltmarsh into shallow depression whilst others end abruptly with a cliff. This is a sign of headward cutting by the creeks. The seaward edge of the *Halimione portulacoides* zone ends abruptly giving way to a short thin grassy stretch along the top of the banks of the Seeping river. The banks themselves are quite steep, steepening with depth. Other than a scattering of *Salicornia* spp. at the top, the banks are bare mud containing vast numbers of the invertebrate *Corophium volutator*. In the upper parts of the banks there is a consolidated sediment surface roughly 30 cm below the soft surface mud. This layer deepens down the bank towards the channel.

3.3.4.2 Sampling Site: Salior's Holme (SH)

Salior's Holme has a shallow creek system. The saltmarsh displays clear vegetation zones moving seaward. These are, from landward to seaward: (1) quite typical high saltmarsh,

grassy mixed community with stands of *Halimione portulacoides* forming frequent small hummocks; (2) a zone dominated by *Puccinellia maritima* and there are numerous pans in the area where this zone grades into the next; a zone that is quite heavily poached with wet ground, and abundant *Hydrobia ulvae* and occasional low-density stands of *Salicornia* spp. and *Spartina anlgica*; (3) a low saltmarsh zone with increasing amounts of *Spartina* forming dense stands separated by sparser patches with more *Salicornia* spp. cover; (4) a pioneer saltmarsh zone with decreasing overall vegetation cover, a marked decrease in *Spartina anlgica* and an increase in *Salicornia* spp.; (5) mudflat; (6) sandflat.

The saltmarsh shows signs of eutrophication through algal blooms in the pools, plus some human sewage. This eutrophication of the saltmarsh is probably largely due to the high grazing density.

3.3.4.3 Sampling Site: Frampton Saltmarsh (FR)

The saltmarsh is own and managed by the RSPB and is also an SSSI.

Frampton is a very extensive saltmarsh and very old frontage (English Nature staff, pers. comm.). The saltmarsh is managed by grazing. The saltmarsh and intertidal flats are currently actively accreting to the extent that the saltmarsh edge is roughly 200 metres further seaward than indicated on the OS 1:25,000 map. Most of this accretion is due to *Spartina anglica* colonisation of the saltmarsh (RSPB staff, pers. comm.).

The high saltmarsh flat is very wide, deep, and diverse, with dense *Halimione portulacoides* stands on the creek tops. A well-developed, distant creek system drains the saltmarsh, converging into two very large, deep creeks at the seaward edge of the saltmarsh. On many of the vertical banks of the creeks distinct laminations can be seen in the sediment.

Moving down the transect the saltmarsh vegetation changes to a Puccinellia maritima-dominated sward. In the lower depressions on the saltmarsh surface monoculture stands of *Spartina anglica* dominated, with occasional scattered *Salicornia* spp. plants.

This low saltmarsh zone is found on large rolling mud banks between the large creeks draining the saltmarsh. The accreting *Spartina anglica* stands are further seaward but large creeks and soft muds prevent access.

3.3.5 North Norfolk Coast

The north coast of Norfolk is a complex estuarine system stretching from Holme-next-the-Sea in the west to Cley in the east. The complexity of the coastal system makes it difficult to split the coastal up into discrete estuaries and is therefore better interpreted as one system, categorised by Davidson *et al.* (1991) as a mesotidal barrier beach. The area comprises a number of sand and shingle recurved barrier structures providing the shelter for saltmarsh and intertidal flat development. The two largest barrier structures are Scolt Head Island and Blakeney Point (both NNR's). Smaller structures also occur at Thornham, Wells and Wareham also enclosing significant areas of saltmarsh (French and Stoddart 1992). These barriers and saltmarshes developed during the Holocene as a result of sedimentation of seaward of a pre-glacial coastline (French *et al.* 1995a; 1995b). Bedrock in the area comprises Cretaceous chalk, overlain in many areas by Pleistocene glacial and fluvio-glacial deposits (French *et al.*, 1995b). The barriers are extending in a westward direction (French & Stoddart, 1992). French *et al.* (1995b) notes that an interesting finding from Funnell and colleagues research is that the present day coastal configuration is largely determined by structures that are inherited from the beginning of the Holocene or earlier.

Fluvial inputs to the coast are minimal indicating that coastal features are dominated by seaward influences, including sediment sources and tides. The main sediment sources for the coastal features (barrier structures and saltmarshes) are thought to be from recession of coastal cliffs both in the area and further east along the Norfolk coast, and offshore glacial material (French *et al.* 1995b). Water turbidity is much lower than the Wash and this is directly reflected in the slower rate of saltmarsh maturation.

The coast is experiencing background eustatic rise at the same time as it is undergoing isostatic down-warping. This low-lying coastal area is therefore increasingly at risk from flooding.

Vegetation on the North Norfolk saltmarshes exhibit clear zonation and primary pans are widespread. This is an indication of the mature nature of these saltmarshes. Some areas of saltmarsh have been reclaimed for agriculture, mostly over the last 350 years (French *et. al* 1995b).

The North Norfolk coast is of great value both in terms of conservation and of research into these kinds of environments and their development, as it is a relatively natural environment with little human modification compared to other estuarine areas in the country. The whole area is classified as the North Norfolk Coast SSSI. The area is also an SPA, and a candidate SAC.

3.3.5.1 Sampling Site: Stiffkey Marsh (SK)

The site is covered by the same conservation designations as those for the wider North Norfolk coast. Locally it is a National Trust managed nature reserve to MHW.

The saltmarsh is split about 600-700 metres out from the landward edge by a shingle ridge that cuts across the saltmarsh. The origin of this feature could not be ascertained but, considering the proliferation of shingle and sand barrier features in the area, it is likely that it is a natural feature. This ridge appears to neatly split the high saltmarsh from the lower intertidal environment.

The lowest intertidal flats are sandy, rising on a low and even gradient. A large creek (Cabbage Creek) bisects the low sandflats at this site, and formed the lower limit of the sampling site. Progressing landward, a thing veneer of mud appears on the sand surface, which is assumed to be an ephemeral feature (French & Stoddart 1992). This zone grades into a ridge and creek pattern with occasional *Fucus spiralis* plants and other seaweeds on the ridges. The ridges and creeks increase intensity as the relief rises, with the ridges becoming colonised by *Salicornia* spp. and *Spartina anglica*. This ridge and creek system begins to break up into a rather scrappy wet, boggy zone in front of the shingle ridge. This zone dominated by *Spartina*; with frequent but sparse *Salicornia* shoots.

On the landward side of the ridge, the habitat is high saltmarsh, all above MHW, with a mature network of quite large, deep creeks. *Halimione portulacoides* is found on creek tops

but towards the back of this high saltmarsh a Halimionetum has developed where the level is higher and the sediment has a higher shingle content. Numerous large primary and channel pans are found throughout the high saltmarsh, with the latter more prevalent in the Halimionetum.

3.3.5.2 Sampling Site: Burnham (BU)

This site is on the landward side of the intertidal environment in the lee of Scolt Head Island. A large tidal channel separates the landward saltmarsh from the saltmarsh on the southern flank of Scolt Head Island. The sampling site is restricted in its landward development by a seawall constructed in 1822 enclosing, what was at the time, saltmarsh for agricultural purposes (French *et al.,* 1995b).

The site is covered by the same designations as those listed for the wider North Norfolk coast above, and locally, is part of a National Trust owned nature reserve.

The gradient of the mudflat increases to a steep rise before levelling off into a gently rising surface of mud banks, cut through by large, meandering creeks. The mud up of the bank-tops is above MHWN and tends to become rather desiccated with geometric cracking appearing during the neap phase of the tidal cycle. Sparse *Salicornia* spp. and *Spartina anglica* shoots are found on these banks. Gradually creeks became more numerous and smaller, in keeping with the dendritic pattern of creek systems in the North Norfolk coast (French *et al.* 1995b). These start to run parallel to each other, perpendicular to the main channel, in the ridge-and-channel pattern seen frequently elsewhere. Small, stunted and sparse *Halimione portulacoides* shrubs are found on the ridges. The gradient here is still considerably higher than on the high saltmarsh.

The gradient gradually reduces in the mid saltmarsh - a zone of short mixed grassy sward with numerous pans primary and depressions, which often contain sparse coverings of *Salicornia*. As the surface height continues to rise, this community grades into the high saltmarsh community. Numerous primary pans occur in this transition zone. The high saltmarsh is dominated *Halimione portulacoides* which have spread out from the creek banks, at times converging across the saltmarsh surface between creeks forming dense stands

forming a Halimionetum (Chapman, 1960). In the wider continuous areas of saltmarsh surface a more diverse high saltmarsh flora is found.

A broad, shallow creek runs along most of the back of the saltmarsh, parallel to the bottom of the seawall. The creek bed comprises fine silty clay. Beyond this creek is the high saltmarsh, which extends for over 0.5 km.

3.3.6 The Deben

The Deben is a mesotidal coastal plain estuary on the south-western coast of Suffolk, East Anglia. The Deben is one of the most northerly of a series of estuaries along this southern East Anglian coastline, stretching from the Ore/Alde/Butely in the northeast, to the Thames in the southwest.

The Deben is a soft sediment estuary. It is a narrow shape with no widening towards the mouth as is common with many coastal plain estuaries. It is heavily used for recreation, in particular boating. The narrow channel is roughly ½ to 1 kilometre wide for much of the length, narrowing up stream at Woodbridge as it reaches its tidal limit. A narrow strip of mudflats fringes the channel. Pioneer and low saltmarsh communities are present on wider intertidal deposits further up the estuary near the town of Waldringfield. Much of the original intertidal area has been reclaimed for agriculture and sea banks along much of the shores of the estuary restrict development of a high saltmarsh environment, apart from very narrow strips in front of the sea banks near the mouth of the estuary.

This estuary is designated an SSSI and SPA.

3.3.6.1 Sampling Site: Deben (DB)

The sampling site was chosen in the middle reaches of the estuary ½ km north of Waldringfield on the western bank of the Deben where low saltmarsh communities have developed across the mudflat in front of the sea bank. Much of the colonisation in this area is due to *Spartina anglica* and it is possible that the spread of this invasive species in threatening the loss in the intertidal mudflat environment in the area. This is a common problem associated with the colonisation of this aggressive species.

Above low water in the channel of the Deben soft mudflats rise gently landwards and around MHWN a pioneer saltmarsh community develops. Broad shallow creeks flowed out across the flats. Landward the creeks rapidly separate into a dense network of broad shallow creeks, ½ - 1 metres wide, cutting through islands of slightly raised sediment surface. The smaller and lower raised areas are colonised by *Salicornia* spp. Where the raised areas are larger *Spartina anglica* occurs, generally forming dense stands in the central areas with *Salicornia* along the creek banks. The central *Spartina anglica* dominated areas tended to be slightly lower than the creek margins giving the raised sediment areas a concave profile. *Hydrobia ulvae* is abundant throughout the area. A shallow creek roughly half a metre wide runs along the back of the saltmarsh parallel to the seabank, but separated from the bank by a narrow *Aster stoniliflora* zone at the foot of the bank.

The site is within the Deben Estuary SSSI and SPA.

3.3.7 Hamford Water

Hamford Water is a mesotidal emabayment on the Essex coast, south of Harwich. It has formed by the deposition of soft sediment in a concave curve of the coastline between shingle spits. It is a shallow bay comprising creeks, islands, sandflats and considerable areas of saltmarsh and mudflat. Saltmarsh covers one third of the bay and the total intertidal area comprising two thirds of the area of the bay. Most of the intertidal flats are comprised of clays and silt. The bedrock in the area is London Clay.

The inlet is notified as an SSSI, NNR, Ramsar Site and SPA. It is an important breeding site for a number of internationally important wildfowl and supports communities of coastal plants that are rare in Britain (English Nature staff, pers. comm.).

A sea bank surrounds the bay on all sides, although the line is not completely continuous and has, in places, been breached.

3.3.7.1 Sampling Site: Hamford Water (HW)

The sampling site is across the intertidal area called The Wade, the area between the mainland to the south, and Horsey Island - the largest island in the bay. The Wade is drained to the east by the Twizzle channel, and to the west by Kirby Creek; both drain round the island into the main channel of the Hamford Water which flows to the north of the island.

The centre of the Wade is very soft mudflat drained by the a network of creeks feeding the Twizzle and Kirby Creek. The sediment surface is strewn with shell fragments from the numerous shellfish within the bay such as *Macoma balthica, Mytilis edulis* and *Ostrea edulis* (Engilsh Nature staff, pers.comm.). Landward across the mudflats *Hydrobia ulvae* is common, but not as abundant as in other sites, such as Frampton saltmarsh in the Wash. Thick green algal mats are common across the flat surface. A low cliff in the mud, exposing consolidated and laminated intertidal sediments, leads to a pioneer saltmarsh community of *Salicornia* spp. and *Spartina* spp. in equal amounts plus *Fucus spiralis* and *Eteromorpha* spp. It is likely that what is being occurring here is a progressive encroachment of *Spartina anglica* into the *Salicornia* spp. zone. A dense network of shallow creeks and pans appears associated with an increase in floral diversity, although still sparsely vegetated. This zone develops into a hummocky, boggy high-saltmarsh community. The vegetation is tall and rank, suggesting that there is no grazing at this site. Further landward *Elymus* spp. begin to dominate the sward and the saltmarsh becomes much more hummocky and peatier in nature. At the foot of the sea bank the vegetation is tall, and the sediment very fibrous and waterlogged similar to the landward edge of the saltmarshes at Wigtown and Caerlaverock.

3.3.8 The Blackwater Estuary

The Blackwater estuary is a macrotidal coastal plain estuary on the Essex coast, south of Colchester. It is the largest in the series of Essex estuaries, north of the Thames and has the fifth largest area of saltmarsh in Great Britain (Burd, 1992). At the mouth of the estuary the Backwater joins with the Clone estuary. The site contains shingle and shell banks, offshore islands, mudflats and fringing saltmarsh. A sea wall skirts the whole of the estuary, enclosing ancient grazing saltmarsh created from high saltmarsh. Despite the loss of high saltmarsh habitats the saltmarshes still display a good zonation.

The saltmarsh in the estuary is known to be eroding at a rate of 0.3 - 1 metres a year (English Nature staff, pers. comm.). 23% of the saltmarsh in south east England has been lost due to erosion between 1973 and 1988 (Burd, 1992). This erosion is the result of a rise in relative sea level of 4-5 mm per year in the last few decades in this area (Pethick, 1993). Leggett *et al.* (1995) discuss the possibility of heavy metal and pesticide pollutants as another cause of saltmarsh decline in the Essex estuaries and Underwood (1997) suggests that sea defence structures have exacerbated these other impacts by preventing landward migration of the saltmarsh system. Part of Northey Island has been used to carry out managed retreat trials during which diatom colonisation of the retreat site was investigated by Underwood (1997).

The estuary is an SSSI, SPA and Ramsar site and forms part of the Essex estuaries cSAC.

3.3.8.1 Sampling Site: Blackwater (BW)

The sampling site is an inland site towards the tidal limit of the estuary across the southern arm of the Blackwater river where the channel splits. The main channel flows north around Northey Island and a much smaller channel, Southey Creek, flows south around the island. At low tide during spring tides Southey creek can run dry. The island is only separated from the mainland to the south by a strip on intertidal roughly 200 metres wide. This site is 3.5 km from the tidal head of the river, which has a tidal channel length of 21.2 km. Hence, this site has a high freshwater influence.

Southey creek flows through very soft intertidal mudflats. The channel has gently sloping sides, and a flat base giving it a watch-glass profile. The landward gradient is smooth, apart from the small cliff between mudflat and saltmarsh. To the north of the channel the mudflats lead up to open stands of *Salicornia* spp. in front of a sea wall around the island. To the south, the mudflats lead up to a low cliff above which there is a narrow low saltmarsh zone. This cliff is the result of erosion due to rising sea level in the area in the last few decades (Pethick, 1993). The low saltmarsh zone is dominated by *Spartina anglica* to its seaward edge with a more mixed, grassy sward towards the back below the seabank. The seabank prevents the development of a high saltmarsh environment, which would otherwise naturally have been present. A number of small creeks bisect the saltmarsh.

3.3.9 Lymington Estuary

The Lymington estuary is a mesotidal coastal plain estuary on the Hampshire coast discharging into the Solent. It is typically funnel-shaped with fine sediments deposited on the broad, shallow flanks of the estuary, much of which has been colonised by saltmarsh assemblages. It is a small estuary draining part of the New Forest through low-lying agricultural land and frequent rural settlements. Currently recreational use is heavy as the whole Solent area is very popular for sailing.

The site falls within the Hurst Castle and Lymington River Estuary SSSI and the Solent and Southampton Ramsar Site and SPA.

Cundy and Croudace (1996) report a rate of relative sea level rise of 4-5.5 mm per year on the Hampshire coast over the last 100 years using radionuclide dating and geochemical analysis of sediment cores. (This rate is the same as that for the Essex coast over recent decades at 4-5 mm per year (Pethick, 1993).)

3.3.9.1 Sampling Site: Lymington (LY)

The sampling site is across the outer eastern saltmarshes of the estuary. In this area a broad deep channel separates the high saltmarsh from the shingle beach on the landward side.

Mudflats end abruptly at this site at a high cliff, 50 - 100 cm high. Away from this cliff the mudflats are smooth, but nearer the cliff, they are disect4ed by numerous flat-bottomed shallow creeks. These creeks have stones and shell fragments in the bottom. Between the creeks the higher mudflat surface appears to be eroding. These ridges form spurs which peter out seawards as the creeks broaden out onto the smooth mudflats. To the east (seaward), and to the north (landward through a beach in the saltmarsh surface) the sediment gets sandier.

At the base of the saltmarsh cliff there are some small blocks of saltmarsh on the lower intertidal surface. This is evidence that the saltmarsh is currently eroding, as would be expected with the rising sea levels described above. The high saltmarsh surface is separated from the land by a broad, deep channel flowing parallel to the coast. On the landward side of the channel there is a shale beach rising up to a cliff roughly 1 - 1.5 metres high. The

saltmarsh is therefore in effect an island being surrounded by a large deep channel to the west and north and the Solent Water to the south and east. There are also a number of small creeks cutting through the saltmarsh from one side to another and many other creeks which end in large, primary and secondary pools within the saltmarsh. The creeks often have low-saltmarsh and pioneer vegetation. *Salicornia* spp. are commonly found in the creek edges, and in the pools, often together with a film of green algae on the sediment surface. Stands of *Halimione portulacoides* are found along creek and pool tops. The proliferation of creeks and pools means than often the vegetated, flat saltmarsh surface appears as small islands, all with vertical cliffs to the creeks and pools surrounding them. On some of the smaller, better-drained saltmarsh sections a Halimionetum has developed.

3.3.10 Poole Harbour

Poole Harbour is a microtidal embayment on the Dorset coast. It covers an area of 35 km^2 and contains numerous small islands. Two spits reduce the mouth of the bay to a passage of roughly 400 metres. Four rivers drain into the Harbour from Cretaceous chalk catchments. The fine sediments within the Harbour are thought to be predominantly fluvial in origin although fluvial input only accounts for 2% of the total low water volume (Bray, *et al.*, 1991).

The northern shore of the bay is heavily populated with the towns of Poole and Bournemouth and associated facilities built right up to the defended shoreline. This is a very busy area with numerous marinas, an international and local ferry terminal and a port. The inner western end of the bay and the southern sores are considerably less modified by human activity, with numerous islands and peninsulas fringed by saltmarsh and varying widths of mudflats, from a few metres to over one kilometre. The main channels through the bay are dredged to keep a navigable channel open for ferries and other shipping traffic.

Holocene relative sea-level change in Poole Harbour has been investigated by Edwards (2001). Results of this study reveal that the area has experience long-term crustal subsidence at a rate of 0.5 mm/yr. Relative rates of sea level rise have increased over the last 2500 years and this is thought to be due to eustatic fluctuations (Edwards, 2001).

Poole Harbour is an SSSI.

3.3.10.1 Sampling Site: Poole Harbour (PH)

The site within Poole Harbour that was chosen for sampling was Lychett Bay, in the north-western corner of the bay. Lychett Bay is just beyond the limit of the built up northern shoreline and one of the least disturbed, and least modified areas with Poole Harbour. The bay is almost entirely filled in by intertidal mudflat sediments, with a sparse, dendritic pattern of shallow channels draining the soft muds into the main channel of Poole Harbour. Moving up the tidal gradient the mudflat is fringed with a *Salicornia* spp. zone, which rapidly becomes mixed with an open covering of short *Phragmites australis* plants. (In parts of Lychett bay a high saltmarsh vegetation zone is present between the *Salicornia* zone and the *Phragmites* beds, but in the western area sampled this additional zone was not present.) Moving landward the relief rises smoothly along with a rising height and density of *Phragmites* to a dense reed bed. This reed bed is, in the main, less than 100 m wide. The reed bed ends abruptly at a small cliff roughly 30 cm high. Heath vegetation is found above the cliff, which is flooded by the highest astronomical tides.

Lychett Bay has no significant human impacts other than the ubiquitous impacts on water quality.

3.3.11 The Exe Estuary

The Exe estuary is a macrotidal bar-built estuary on the south Devon coast, south-west England. It is 10 km long and only 1 - 2 km wide for its whole length. The estuary is enclosed by a spit extending north from Dawlish, toped by sand-dunes. The estuary is defended with seawalls and banks for much of its length. This constrains the intertidal environment to mudflats only, with virtually no higher tidal environments. On the western shore embankments protect the railway line. On the east it has been constructed and maintained for a mixture of land reclamation, road protection and flood defence purposes. The estuary contains *Zostera* beds that provide an important feeding ground for Brent Geese and other shorebirds (Fox, 1996).

In much of the estuary the sediment consists of very soft muds, whilst in some parts accumulation of shell fragments from the many shellfish in the area created firm ridges and substrates.

The Exe estuary is an SPA and Ramsar site and an SSSI.

3.3.11.1 Sampling Site: Exe (EX)

This sampling site is in the lower-middle reaches of the Exe estuary on the eastern shore just south of the small town of Lympstone.

Low tide exposes intertidal muddy sandflats, containing a high proportion of shell fragments reflecting the abundance of shellfish in the area. A high seawall at the back of the intertidal flats (protecting the railway line) prevents any transition to higher tidal environments. Near the river channel the flats are very soft and muddy with little to no shell fragments. *Zostera* is found at the lowest points on the flats. Progressing landward distinct seaweed zones occur parallel to the river channel. The sediment then gets progressively firmer as shell fragments mix in with the soft muds. The intertidal flats become increasingly firm in a landward direction reflecting the increasing proportion of shell fragments within the substrate. At the back of the intertidal flats there are three distinct ridges parallel to the sea wall, each leading to a step in altitude.

Quite a large amount of sewage-related debris was seen on the intertidal flats, suggesting significant eutrophication of the estuarine waters.

3.3.12 Bridgewater Bay

Bridgewater Bay is a macrotidal embayment on the Somerset coast of the Bristol Channel. The hypothetical line of division between the Severn Estuary and the Bristol Channel is drawn north of Bridgewater Bay (from Sand Point (ST 317 659) on the English coast to Lavernock Point (ST 190 679) on the Welsh coast). In terms of diatom data analysis this site is included in the Severn estuary *region*, but for the purposes of site description Bridgewater Bay is treated as a separate estuary. The tidal range in this area is classified by Davidson *et al.* (1991) as 'exceptionally large', with a MHWS measurement of 12.2. metres (Hydrographer of the Navy, 1997). The location of the Bay also exposes it to strong offshore winds.

Bridgewater Bay consists of extensive muddy sand areas of intertidal and subtidal sediments, including saltmarsh. Saltmarsh is able to develop here due to the dissipation of the strong tidal and wave energy over the broad intertidal mudflats. Within the Bay there are areas of erosion, deposition and stability (Killops and Howell, 1988; Kirby, 1994). The fine sediment deposits are in contrast to the general character of the Bristol Channel, which is dominated by sand and gravel beaches in the intertidal compared to the mudflats and saltmarshes further north in the Severn Estuary. Bridgewater Bay contains one of the only (and certainly the largest and most significant) subtidal mud deposit in the whole of the Severn Estuary and Bristol Channel system. This area acts both as a sink and a source of fine sediments for the whole system (Kirby, 1994).

Bridgewater Bay is notified as an SSSI, NNR, Ramsar Site, SPA and pSAC.

3.3.12.1 Sampling Site: Bridgewater Bay (BW)

The sampling site traverses an intertidal area called Steart Flats, to the west of the mouth of the Parrett River, roughly 1 km west of the old parish boundary fence line across the intertidal flats, perpendicular to the shore. The intertidal flats at Steart Flats are up to 3 km wide and 2 km in the area sampled. The wide mudflats develop a parallel ridge and creek pattern moving landward, that is perpendicular to the tidal front. The height differential between the creeks and the ridges, and the firmness of the sediment on the ridges, increases up the tidal gradient. The gradient then increases and these mud-ridges and creeks give way rather suddenly to a stretch of sandflat of increased gradient. The sand appears to be engulfing the pioneer zone above it. Small, eroded blocks of sediment from the saltmarsh are strewn across the surface of the pioneer saltmarsh zone. This zone of erosion within the intertidal environment is very similar to that seen at the Wentloodge site, some distance north in the Severn estuary.

Spartina anglica dominates the saltmarsh zone that is experiencing tidal erosion, with slightly elevated islands of saltmarsh dominated by a more mixed saltmarsh flora. *Spartina anglica* stands, although remaining dense within the stands themselves, begin to decrease in frequency up the saltmarsh and the species found on the raised surfaces in the *Spartina anglica* zone come to dominate in the next zone. The saltmarsh hear, and in the Spartina zone has a very uneven, rough surface. A high saltmarsh community has developed above this zone containing numerous patches of *Triglochin maritima* and *Plantago maritima*. The saltmarsh

does not appear to be heavily grazed, but there are occasional hoof prints suggesting that some grazing does take place, and indeed the sward height is lower than would be expected were the saltmarsh completely un-grazed. This short sward is dominated by *Puccinellia maritima*. A gabbion-basket sea defence structure runs along the back of the saltmarsh, separating it off from the reclaimed agricultural land beyond. On the eastern side of this sampling site, towards the old parish boundary fence line, there is a *Phragmites australis* bed that widens eastwards.

3.3.13 The Severn Estuary

The Severn estuary has a very large tidal range, with a mean spring tidal range of 13.2 metres (Hydrographer of the Navy, 1997). The Severn is also one of the largest estuaries in Britain. The large Atlantic tide is amplified in the Severn by the funnel-shape of the estuary which also leads to the occurrence of a tidal bore. The Severn is a very high-energy estuary due to the large tidal currents. This results in continual redistribution of sediments within the estuary on every tide (West and West, 1989). As a result, turbidity levels are high (see Kirby, 1982). Killops and Howell (1988) estimate that sediment up to sand grade is mobile most of the time.

The Severn contains extensive intertidal flats and saltmarsh, which are made up of four distinct morphological units (Allan and Rae, 1987). The saltmarshes of the Severn are currently undergoing net erosion due to a period of sea-level rise (Kirby, 1994). Allen and Rae (1988) report widespread lateral throughout the estuary of up to 1.0 metres per year. This is evidence by the saltmarsh cliffs at Wentloodge and Aust Sampling Sites.

Large urban and industrial developments along the shores of the Severn have led to significant modification of the shorelines, as well as a suit of pollutants within the sediments (French, 1993). Nevertheless, the biodiversity of the estuary is good (Wiseman, pers. comm.), reflected in numerous conservation designations, including the Severn estuary SAC.

3.3.13.1 Sampling Site: Wentloodge (WL)

The Wentloodge saltmarsh is situated on the lower reaches of the Welsh shore of the Severn Estuary, to the east of Cardiff. The saltmarsh is grazed in the summer, and apparently the

vegetation expands forward every summer, and then the saltmarsh is eroded back every winter (O'Brien, *pers. comm.*).

The high saltmarsh is quite badly poached and very hummocky with a diverse flora. There is a small, but marked, drop in elevation from the high saltmarsh to an eroding section of saltmarsh consisting of parallel ridges and creeks running perpendicular to the shore. The vegetation on the ridges is dominated by *Plantago maritima*, although the cover is sparse. The end of the eroding zone is quite abrupt, giving way to a smooth mudflat substrate extending out to the channel of the Severn estuary.

3.3.13.2 Sampling Site: Aust (AU)

This Sampling Site is situated in the middle of the Severn estuary, between the two Severn road bridges. The transect is taken across was taken across Aust Wharf saltmarsh perpendicular to the road (B4461). The site is an SSSI.

The high saltmarsh is relatively flat with a very shallow gradient towards the Severn channel. This gradient increases sharply through the mid and low saltmarsh habitats giving rise to a sharp incline down onto the soft mudflats beyond. The high saltmarsh vegetation is a short grassy sward that is grazed. Once the gradient begins to steepen, *Spartina anglica* starts to mix in with the *Puccinellia maritima*, leading to a *Spartina anglica* pioneer saltmarsh zone. There are signs of erosion at the boundary between the low saltmarsh and the mudflat with small blocks of low marsh scattered for two meters in front of the marsh. These would appear to be derived from the steep-sided creeks that drain the saltmarsh. The mudflat sediments are very soft with a consolidated layer at a depth of 8 cm within the upper mudflat.

3.3.13.3 Sampling Site: Arlingham (AR)

This sampling site is in the upper reaches of the Severn Estuary across a sandbank on the inside bend of a tight meander, opposite the town of Newnham (on the outside bank). The whole bank comprised realtively coarse sand, with a file of mud on the surface, which is assumed to be ephemeral.

3.3.14 The Mawddach Estuary

The Mawddach estuary is a mesotidal bar-built estuary on the western coast of Wales. The Mawddach has a classic funnel-shape associated with bar-built estuaries. The estuary reaches a maximum width of 2 km, but the mouth is restricted by the development of the bar to a passage of 300 metres. The bar that stretched across the mouth of the estuary is comprised of sandy sediments forming a dune system whose continual development is constrained by sea walls. In the lee of the bar a large area of shifting intertidal sands has accumulated, with grazed saltmarsh fringing the intertidal flats along the southern shore. The sediment has predominantly sandy reflecting the hard geology of the rural catchment.

3.3.14.1 Sampling Site: Mawddach (MD)

The sampling site is situated on the southern shore of the estuary in the lee of the bar. A flood embankment protecting a large area of low-lying reclaimed land beyond, restricts landward development of the saltmarsh habitat. The saltmarsh is grazed and towards the back of the marsh the flora resembles a mesotrophic grassland. Small shallow creeks drain the saltmarsh across a shallow gradient. The vegetation changes gradually through mid saltmarsh communities to a low, pioneer marsh community consisting of a sparse covering of *Salicornia* spp. A broad, shallow sandy creek, running parallel to the shore separates the low saltmarsh from the intertidal sandflats beyond.

3.3.15 The Solway Firth

The Solway Firth is a large firth on the western coast of Britain straddling the English and Scottish border. For the purposes of this study the Solway Firth is described as the estuary of the Eden and Esk rivers. This is often referred to in literature and conservation designations etc., as the inner Solway. But, as Wigtown Bay and Skyreburn Bay, by that latter definition, fall within the outer Solway Firth, it is better to avoid confusion and describe the Solway Firth merely as the area of the firth that is estuaries in nature. For the purposes of diatom data analysis the Sampling Sites of Wigtown and Skyreburn Bay are combined with Caerlaverock and Bowness-on-Solway to form the Solway Firth region. Wigtown and Skyreburn Bay are treated as separate estuaries for the purposes of site descriptions.

The Solway Firth is a macrotidal complex estuary. The origin of the Solway basin's complex structure lies in the closure of the Iapetus Ocean caused by the collision of the Laurentian and Avalonican continents through the late Sillurian and early Devonian (Solway Firth Partnership, 1996). Since then the area has undergone many changes. Successive glaciations have altered the surface geology many times. The underlying bedrock of the Solway Firth estuary is Carboniferous. This is overlain by many metres of boulder clay which it turn is overlain with glacial drift. This material is presumed to be the major source of material for the development of the extensive sandflats and saltmarshes of the inner Solway (Solway Firth Partnership 1996). Marine sediments lie on top of the glacial drift. The sediments within the estuary are sandy, unusually so for an estuary. This is due to the sediments being derived from the erosion of glacigenic material deposited in the basin and the Solway's catchments in the Devensian.

Chapman (1941) describes all the saltmarshes within the Firth as one geographical unit. However, Harvey and Allan (1998) point out that this hides a great deal of geographical variation in saltmarsh flora within the Firth due to the heterogeneous coastline.

Spartina anglica colonisation has reached the Solway Firth, but as yet is only present at low densities in a small number of sites. Although *Spartina anglica* is found further north in the Cromarty Firth and the Eden estuary, for example, the outer Solway Firth is the only place in Scotland where *Spartina anglica* is abundant. A number of other species of flora and fauna reach their northern limit in the Solway and its distinctive and diverse flora and fauna has led to its designation as an SSSI, SPA, Ramsar site and candidate SAC.

The Solway Firth is often cited as one of the least developed large estuaries in northern Europe (e.g. Solway Firth Partnership, 1996). Very little of the coastline is constrained by artificial sea defences, hence sediment movements and intertidal habitat development continue unmodified over much of the Firth. However, some drainage has meant that much of the higher saltmarsh has been lost to agriculture, and consequently, despite the relatively un-tampered with nature of the estuary, very few examples of fully natural transitions from intertidal through to terrestrial habitats exist. Then Solway has not been wholly without industrial influences. Industrial development in coal and steel along the coast of Cumbria in the 19th and 20th centuries led to a rapid decline in water quality and biodiversity. It also led to marked modification of shoreline sediment movements on the southern shores due to the

dumping of coal and steel slag throughout this period. The geomorphology of this shoreline is still thought to be out of equilibrium, as this artificial material is still being eroded and carried up the estuary by long-shore drift. In more recent years water quality has significantly improved and the estuary is slowly moving towards its former status ecologically.

One further influence on the estuary, which may affect the diatom flora, is the occurrence of raised levels of radioactivity in the waters and intertidal sediments. This is due to discharges from Chapel Cross nuclear power station within the firth and, much more significantly, Sellafield a few miles further down the Cumbrian coast. The effect of the raised level of radioactivity has been and continues to be the subject of much research (see Solway Firth Partnership, 1996). However, there is no conclusive evidence to suggest that these levels have affected the flora and fauna of the estuary.

2.6.15.1 Sampling Site: Bowness-on-Solway (BS)

This site is on the southern shore of the Solway Firth and is an RSPB Nature Reserve and an SSSI, as well as falling within the SPA Ramsar and cSAC designations for the Solway Firth.

There is a large embankment along the back of the saltmarsh. At the base of the bank there is a zone vegetated with *Juncus* and *Elymus* species, and with deep, narrow creeks in places. As the gradient lowers slightly the habitat changes quite abruptly into high, grazed, saltmarsh vegetation. Well-developed creeks run through the saltmarsh and there are deep pans on the surface. The saltmarsh comes to an end at a cliff with eroded blocks scattered in front. The intertidal flats were quite muddy near the cliff but the silt content decreased rapidly seaward until the flats were purely sand. The sand flat was almost a kilometre wide at low water.

Beyond grazing and the soft embankment at the back of the saltmarsh, human influences have been, and still are, negligible.

3.3.15.2 Sampling Site: Caerlaverock (CK)

Caerlaverock is a NNR encompassing the saltmarsh and intertidal flats south east of the mouth of the river Nith; one of the river estuaries nested within the estuary of the Solway

Firth, as described above. The only significant human modification is the grazing of sheep and cattle on the saltmarsh during the summer months.

There is a gentle gradient across the saltmarsh. At the back of the marsh the vegetation is quite rough with mixed grasses and dominated by rushes, finally giving way to gorse bushes which grade into woodland beyond. The ground at the back of the saltmarsh is peaty. The back of the saltmarsh, in particular, shows signs of heavy poaching in places. This grades into the usual mixed saltmarsh community dissected by numerous well-developed creeks. There are also numerous pools. The saltmarsh ends abruptly at a cliff. The height varies between ~ 40 cm and 100 cm. In 5 metres there occurs a second, lower cliff. The two cliffs expose well-laminated sediments. In front of the second cliff there are eroded blocks of saltmarsh and patches of pioneer saltmarsh community. Near the cliff erosion zone the sediment is quite muddy. However, the sand content increases quickly across the flats. There is a large, deep sandy creek winding across the flats to the Solway waters. The bottom of the creek was very muddy and covered with many thousand *Corophium volutator*. The sandflats beyond continue for well over a mile to the low water channel of the Solway.

3.3.16 The Water of Fleet

The Water of Fleet is a small estuary on the southwest coast of Galloway, Scotland, known as Fleet Bay. Fleet Bay drains into Wigtown Bay. The estuary is classified as a macrotidal fjard by Davidson *et al.* (1991). The bedrock is metamorphic and is Ordovician and Silurian in origin. This is overlain by boulder clay and, in the northern tip of the bay, by raised beach and warp deposits (Solway Firth Partnership, 1996).

The sediments are predominantly sandy with varying proportions of shell fragments derived from shellfish living in the highly productive intertidal and subtidal substrate.

The estuary has a high proportion of *Spartina anglica* and, along with Auchencairn Bay further east along the Galloway coastline, has the highest density of *Spartina anglica* in any Scottish estuary (Davidson *et al.*, 1999).

There has been little artificial modification of the bay apart from some sea defence, protecting sections of the A75 that skits around the top of the bay along the raised beach platform. The

only other significant human influence is the presence of grazing on the saltmarsh within the Bay.

3.3.16.1 Sampling Site: Skyreburn Bay (SB)

This bay forms the northwest corner of the Fleet Bay. A the name suggests, the Skyre burn drains through the sampling site to converge with the Water of Fleet further out in Fleet Bay.

The saltmarsh at the site is grazed and is places the ground is quite heavily poached. There is saltmarsh to either side of the Skyre burn as it enters the bay under the A75 road bridge (the road runs around the head of the bay). The sampling site was chosen on the saltmarsh to the south of the channel of the burn. Here the saltmarsh is backed by a fine sandy beach two to four metres wide which gives way abruptly to a wooded slope up to the A75 road. The saltmarsh is hummocky and contains a dense network of shallow creeks. *Spartina anglica* is common in the creeks and pools and forms dense single species stands over much of the lower saltmarsh.

Saltmarsh vegetation is brought to an abrupt end by a linear shale ridge running parallel to the coastline. The ridge is made up of baltic tellin and cockle shells. Both these bivalves are abundant in the sandflats in the bay suggesting that the ridge is a natural feature. Seaward of the ridge the sediment is predominantly sandy with a high shell-fragment content and a fine veneer of silt on the surface. Isolated islands of *Spartina anglica* occur in this zone, as well as occasional *Salicornia* spp. Continuing out towards the centre of the bay the sediment becomes progressively coarser. This lower intertidal zone is rich in tellin species and cockles. *Arcnicola marina* is present but at low density.

3.3.17 The Cree Estuary

The Cree estuary is a macrotidal fjard on the southwest coast of Scotland in Galloway. The Cree estuary broadens out into Wigtown Bay, which also receives freshwater from the river Baldnoch and the Water of Fleet. The site sampled is only very slightly north of the outflow of the river Baldnoch into Wigtown Bay. As such it could be argued that the site should be classified as part of the Baldnoch estuary. However, as Wigtown Bay is essentially the estuary of the river Cree, and the Baldnoch is a much smaller river, it is sufficient for these

purposes to categorise the sampling site as being within the Cree estuary. When referring to the Cree estuary this is taken to mean the area delineated as the Cree estuary by Davidson *et al.* 1991 which does include the mouth of the Baldnoch.

The bay contains extensive intertidal mud and sandflats, and saltmarsh and supports a wide variety and number of migratory and permanent populations of wildfowl and waders. Wigtown Bay is notified as a Local Nature Reserve. The saltmarshes have been grazed for many centuries giving the grassy high saltmarshes their closely-cropped lawn appearance.

3.3.17.1 Sampling Site: Wigtown (WT)

The sampling site is below the town of Wigtown on the western side of Wigtown Bay. The saltmarsh is up to 1 km wide below Wigtown, in the area sampled, although the extent of saltmarsh has been artificially increased to this size. Breakwaters were constructed in the past to increase the amount of saltmarsh available for grazing. The river Bladnoch used to flow into the bay across this section of saltmarsh, but the course was artificially diverted south over 200 years ago, away from this area of saltmarsh. It is grazing saltmarsh, both historically and currently for cattle and sheep, creating a short, lush, green sward for much of the high saltmarsh surface.

Peat is accumulating at the very back of the high saltmarsh surface, in front of a low embankment leading to a dismantled railway line. In front of this peaty zone the high saltmarsh flat has a number of visible vegetation zones. These are zones dominated by *Juncus geradii* followed by a distinctive zone dominated by *Pucinellia maritima* which grades into a mixed high saltmarsh flora for the rest of the saltmarsh surface. The wide saltmarsh is dissected by a number of large deep creeks, which have been modified to provide adequate drainage for the site.

The saltmarsh surface comes to an abrupt end at a cliff roughly 100 cm high. The cliff exposed finely laminated sediments. The cliff is clear evidence of erosion of the upper saltmarsh, and there is some accumulation of eroded sediment at the foot of the cliff. In front of this cliff there is a pioneer saltmarsh zone colonised by a variety of low saltmarsh plants. The pioneer saltmarsh consists of species better adapted to frequent tidal inundation than some of the other species found on the higher saltmarsh, such as *Armeria maritima*, *Aster*

tripolum, *Cochlearia officinalis* and *Puccinellia maritima*. Moving away from the saltmarsh cliff, this diverse pioneer marsh is replaced by a *Salicornia* community. The sediment here is muddy sand. As the height gradually drops towards sea level, the sediment become less muddy, and more sandy and *Aemicola maritima* casts beginning to appear. These are particularly abundant at the top of the bank of a large, impassable creek - the union of a number of creeks draining the saltmarsh behind.

CHAPTER FOUR

METHODS

4.1 Introduction and terminology

This chapter describes the various field, laboratory and statistical techniques employed in this study. The method used to sample intertidal sediments is a crucial aspect of data collection. Before the training data set could be collected the most appropriate method and depth for obtaining sediment samples for diatom analysis was determined and this process is described below. There then follows a description of all other methodological approaches.

Table 3.4, in the previous Chapter, introduces the terminology used to describe the samples and the sites. This is needed in order to ensure consistency and clarity not only in the description of the methods, but in the description and analysis of the results.

4.2 Intertidal sediment sampling techniques

Traditionally sedimentary environments have been sampled using various coring techniques and in intertidal environments syringe-coring methods have been frequently used to sample the top few centimetres of sediment (e.g. Aleem, 1950; Colijn and Dijkema, 1981; Joint *et al.*, 1982; Plante *et al.*, 1986). Wiltshire *et al.* (1997) provide a brief discussion of the problems of intertidal sediment sampling techniques. The main problem with any coring technique is the potential distortion and compaction of the sediment as the core tube is driven through the sediment, especially in wet, unconsolidated sediments such as are found on intertidal flats. Freezing the cores, for example to enable very fine sectioning of the material, can distort the material even further, especially when dealing with very wet sediment (see Rutledge and Fleeger, 1988) whilst traditional larger coring equipment is generally impractical for the purpose and is particularly ineffective at preserving the structure of the upper layers of wet sediments (discussed in Parker 1991). The core diameter is also of importance. Whilst large cores are thought to lead to less distortion (see Rutledge and Fleeger, 1988) smaller cores can

be more reliably sectioned at fine intervals when dealing with fresh sediment with high water content.

With syringe-type coring techniques it is common practice to pull up with the piston whilst the cylinder is driven into the sediment in order to minimise compaction. Hargis and Twilley (1994) suggest the further precaution of a clear cylinder in order to be able to watch the operation to ensure the right counter-pressure is maintained.

Although Joint *et al.* (1982) use the syringe-coring method to sample wet mudflat and sandflat sediments and then section the core (wet) at millimetre intervals using a screw thread and razor blade, Wiltshire *et al.* (1997) still criticise this 'advanced' syringe coring method for only really being reliable in sandy sediments.

Other intertidal sampling methods involve taking simple surface scrapes. This is not appropriate for this study for two reasons. Firstly it is very difficult to sample to a consistent depth with this method and secondly, it is only for the removal of the surface sediments, not the subfossil community. Simply digging deeper samples out would not be precise enough when repeating the method over scores of individual Sampling Points.

Other methods for sampling wetland and intertidal sediments involve freeze sampling, such as Anderson (1980) and Knaus and Cahoon (1990). A new *in situ* freeze-sampling method devised specifically for sampling intertidal surface sediments has been published by Wiltshire *et.al.* (1997). The method is called the Cryolander and involves placing a small tube on the surface of the sediment with a gauze mesh half way up the tube supporting cotton wool onto which liquid nitrogen is poured. This technique freezes the surface sediment without the disruption of a core.

4.3 Diatom sample depth

Quite often sampling techniques go unchallenged, if, in fact, they are even adequately described in the first place. MacPherson and Lewis (1978) raised this issue in relation to studies of recent sediments in estuaries with the question 'what are you sampling?'. This research project requires the collection of a large data set of subfossil diatoms from estuarine

intertidal environments. In the collection of the modern training set of diatoms, being aware of exactly what to, and what is being sampled is of utmost importance. There are two key reasons for this degree of precaution in sampling that relate to taphonomy and intertidal sedimentation characteristics.

Owen (1979), Wilson and Holmes (1981) and Simonsen (1967), amongst other authors, stress the importance of distinguishing between live and dead diatoms in ecological studies in estuarine sediments in order to avoid the inclusion of allocthonous material in the interpretation and analysis. Other studies, whilst not distinguishing between live and dead diatoms, do make attempts to omit allochthonous species from the analysis, e.g. Vos and de Wolf (1988, 1993a). In this current study it is the characteristic assemblages of the indicative fossil environments that are of interest. The fossil record is the end result of taphonomic processes such as breakage, transport and dissolution and will, therefore, contain material that is allochthonous to the environment it was deposited in (see section 2.6.3 for further details). Sherrod *et al.* (1989), in their study of the taphonomic implications of subrecent intertidal diatoms (from St. Catherines Island, Georgia), discuss how the ephemeral living diatom community 'may bear very little similarity to the time-averaged and taphonomically overprinted death assemblages'. The surface, living diatom flora, or 'active layer' (MacPherson and Lewis, 1978), in such intertidal environments, at any one time, is a transient community that varies within and between seasons (Wilkinson, 1980). A sample isolating this assemblage alone would give a very biased representation of the characteristic flora of that particular environment, as found in the fossil record.

It is, therefore, necessary to obtain a more temporally homogenised sample and, if possible, not to include to surface blooms present at the time of sampling. It is, in fact, the subfossil diatom assemblage that is of interest in this study as this is the assemblage that is the direct analogue of the fossil assemblage on which palaeosealevel reconstructions are based. Zenetos (1990), in a study of molluscan taphonomy from the Eden estuary, Scotland, uses the term subfossil to 'denote remains of animals found laying or buried in sediment, that are not strictly recent but not "prehistoric" either'. This can be extrapolated for any fossil organism to include diatoms, and serves as an adequate definition here. This is the assemblage used for the creation of a modern reference set of intertidal diatom assemblages in previous smaller scale studies such as Hemphill-Haley's study in Willapa bay, Washington (1995b) and Zong and Horton's six UK sites (1999).

The second reason for caution in what we are sampling in the intertidal environment is that sedimentation does not always follow a pattern of continual accretion. Whilst estuaries are continually evolving, with either an overall tendency towards accretion or erosion, many factors can cause a change to the reverse tendency, and even during an overall period of accretion, sediment movements within intertidal areas are continually occurring with the tidal currents. With this in mind, if samples are collected from too deep into the sediment, it is possible that the sample obtained actually accumulated under quite different environmental conditions, e.g. mudflat, rather than high marsh.

Clearly, then, there is a real problem over what, exactly, to sample, especially given the variety of tidal ranges, energy and orogeny of the estuaries of Britain. Research has shown that live diatoms are concentrated in the top 1-2 mm (Aleem, 1950; Admiraal *et al.*, 1982), although it is possible that some species can be mobile to depths of up to 4-5 cm. The subfossil zone may, as a result, contain live diatoms. Pinckney *et al.* (1994), in an analysis of the vertical distribution of epipelic diatoms in the intertidal environment found diatom migration to be limited to the upper 3 mm with 33% of the total biomass concentrated in the upper 1 mm. However, Paterson (1986), using a sampling method able to recover vertical samples to a thickness of 0.2 mm, discovered that epipelic diatoms are distributed mainly within the surface 1.6 mm, before and after migration to the surface (see section 2.6.2.5) but that after dawn, with the tide out, there is a massive accumulation in the top 0.2 mm. This indicates that sampling undertaken in daylight with the tide out (clearly the only practical time to sample) should ensure that the majority of motile living diatoms are concentrated in the top 0.2 mm. A distribution of some live diatoms to depths greater than 1.6 mm is characteristic of the environment being sampled and these are unlikely to be present in a large enough degree to bias the sample to such a degree that it bears more resemblance to the ephemeral living assemblage.

A variety of approaches to sampling have been adopted by the small number of previous studies that have developed a modern data set of estuarine diatoms as an aid to palaeoenvironmental reconstruction. Hemphill-Haley (1995b) took the top 1-2 mm in over 80 one-off samples in Willapa Bay, Washington, to ensure the modern flora was obtained. Juggins (1992) took surface scrapes of the top 1-2 cm from intertidal sediments in the Thames

estuary. Zong and Horton (1999) took seasonal samples over a 5 cm surface area to a depth of 1 cm deep and homogenised the seasonal samples.

All are valid for the purposes of the particular study but in this instance, as well as using information available in the literature, an investigation was undertaken to determine the appropriate sampling depth to use here. The problem with a consistent sampling depth for all Sites in the study is the fact that the different tidal regimes, energy and sediment characteristics of the Sites ultimately means the appropriate subfossil layer may be found at and over different depths. Some back marsh areas may be accreting gradually over recent time with very little erosion containing a small discrete subfossil layer, whilst open mudflats in high-energy environments such as the Severn may see large amounts of sediment redistribution with every tide. Each environment will, however, develop eventually into a fossil environment and it is hoped that these differences may be drawn out in analysis. In the light of this variety the aim of ascertaining the appropriate consistent sampling technique may be simplified to sampling the layer that is below the active layer but above any consolidated older sediments that may have been laid down in a different depositional environment.

In order to address the above issues, a pilot study was undertaken to assist in ascertaining the appropriate sampling depth.

4.3.1 Sampling depth pilot study

4.3.1.1 Sampling method

In order to establish the most appropriate sampling method for the collection of the samples for the training data a Cryolander and a clear, plastic syringe-corer of one-inch diameter were constructed and tested on sediments from the small back-barrier estuary of the Aln, Northumblerland.

The Cryolander was found to recover samples with excellent vertical preservation, but it took between 20 minutes and half an hour to freeze a full 2 cm depth of sample. The syringe corer appeared to work very effectively in sandy and muddy sand sediments and could perform reasonably well in wetter, muddier sediments as long as the corer was operated with great care and vigilance, especially in maintaining the right counter-pressure. The syringe corer could

also be used to take deeper samples, allowing for short (up to 8 cm) cores to be retrieved providing material for further detailed study of the sites.

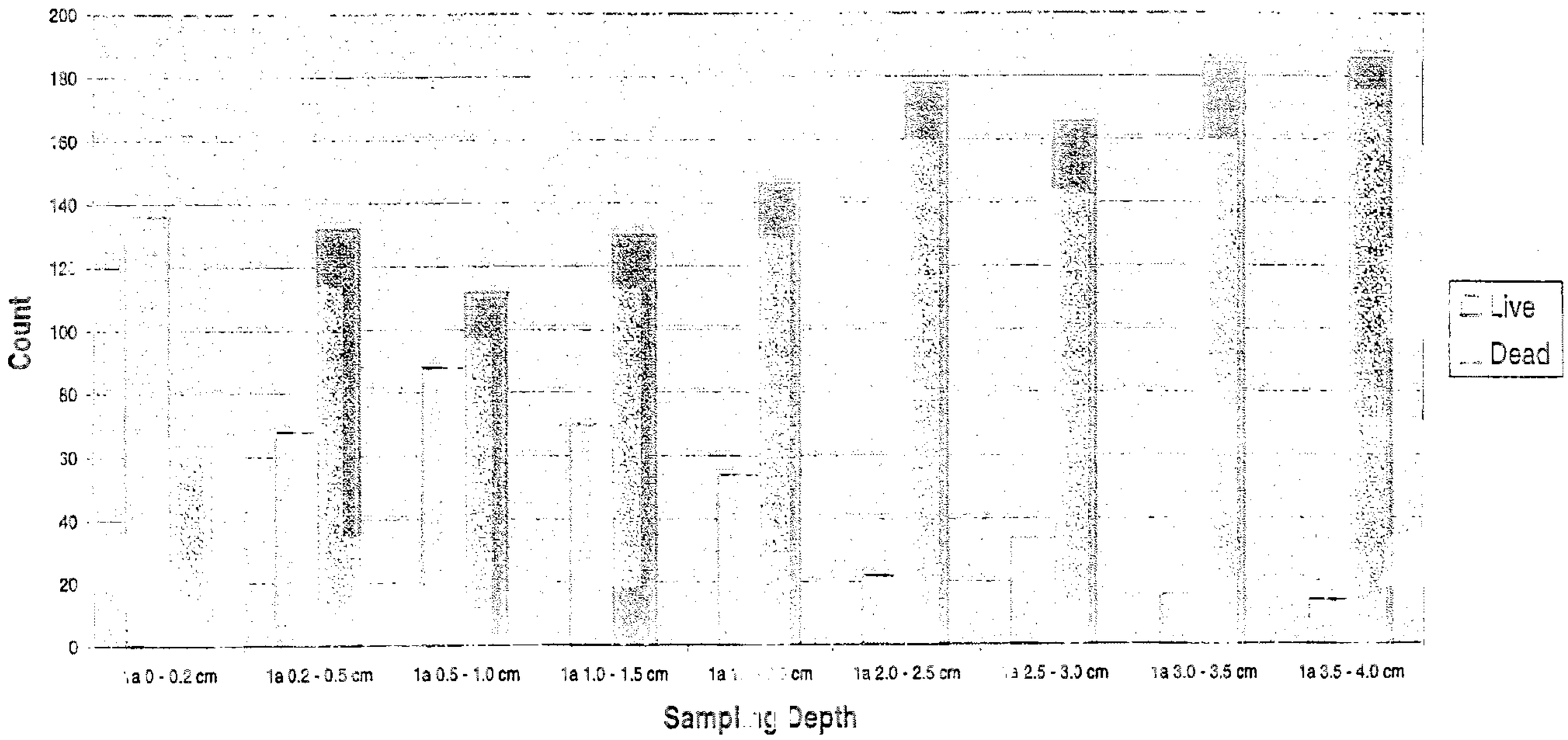
In theory, the Cryolander would have been ideal for the purposes of this work. In practice, however, the slow sample retrieval time, shallow sample retrieval depth and volume and weight of liquid nitrogen that would need to be transported to adequately sample all the Sampling Points at each Site rendered the technique impractical for the purpose. A further consideration was the need to keep the samples frozen until such time as they could be sectioned in a laboratory, which, again, was not feasible when travelling long distances from site to site over a period of days. Accordingly, whilst this method is very effective for the work it was designed for, namely the retrieval of high-resolution intertidal surface sediment samples, it is not considered appropriate for the work in question.

Ultimately the syringe-coring method was chosen over the Cryolander because of the practical problems of the Cryolander outlined above. As long as the technique was executed with due care and attention it was felt to be adequate for the collection of the samples needed.

4.3.1.2 Results of the pilot study

Replicate cores were taken from three different environments within the Wash estuary at the Sailor's Holme Sampling Site using the hand-held syringe corer described in section 4.3.1.1. The three environments sampled were high saltmarsh flat, middle saltmarsh and open mudflat. The cores were then sectioned at 0-2 mm, 2-5 mm intervals, then at 5 mm intervals to a depth of 4.0 cm and all samples were preserved with Lugol's Iodine. Slides of the preserved material were mounted and 200 diatoms counted as live or dead.

The results of the counts are presented in Figures 4.1 - 4.3. As would be expected all six cores show a marked increase in the proportion of live diatoms in the top layer, 0 – 2 mm. All six cores contain live diatoms in the deepest sample, 3.5 – 4.0 cm. The high marsh cores showed the lowest proportion of live diatoms in general, this probably reflects the fact that it is a more hostile environment with fewer species adapted to its conditions leading to a higher proportion of dead autochthonous and allochthonous material. As the high marsh floods much less frequently than the other two environments the firmer and in general drier surface would also inhibit motile diatoms moving as deep into the sediment as has been observed in



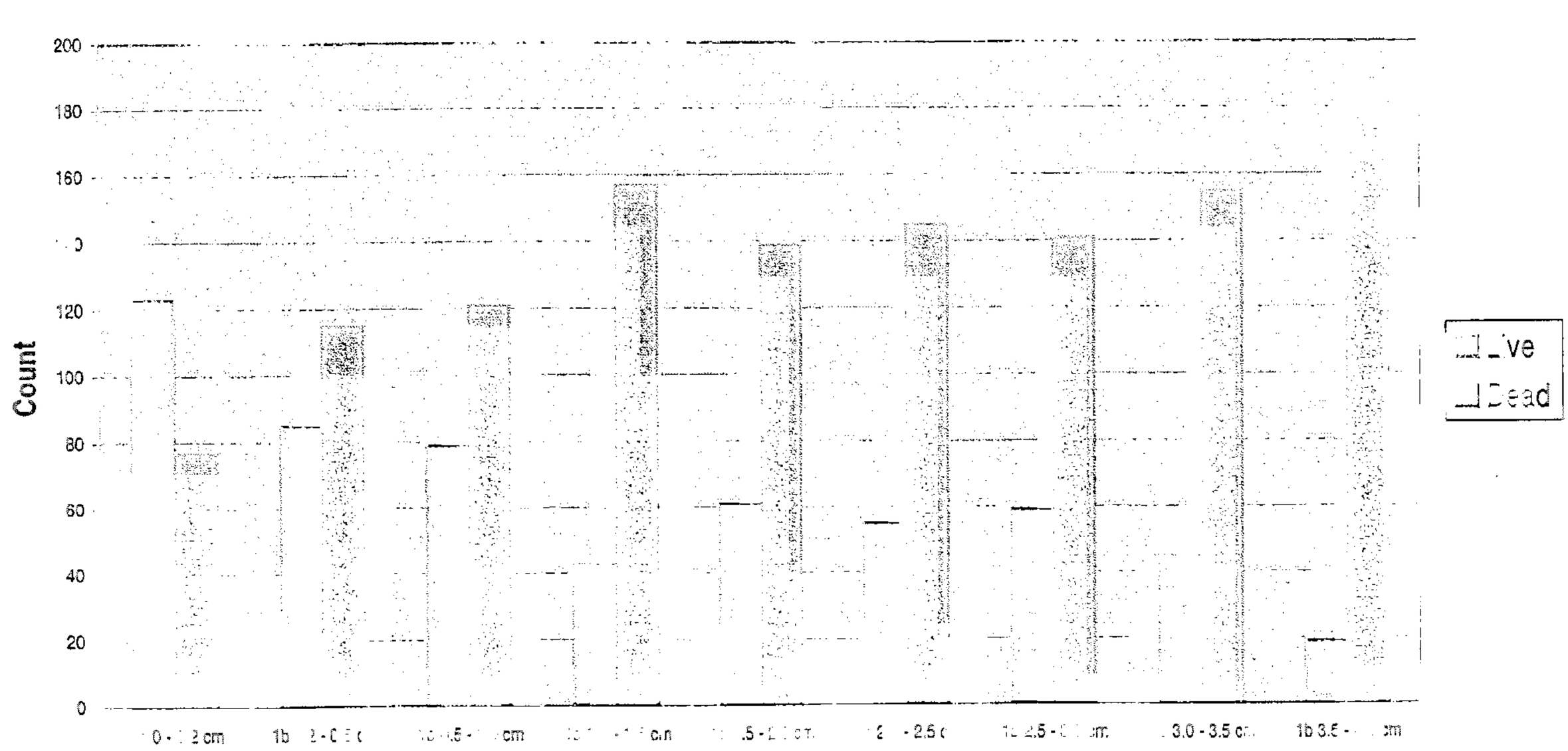


Figure 4.1 Live and Dead Counts Sampling Point 1, high marsh

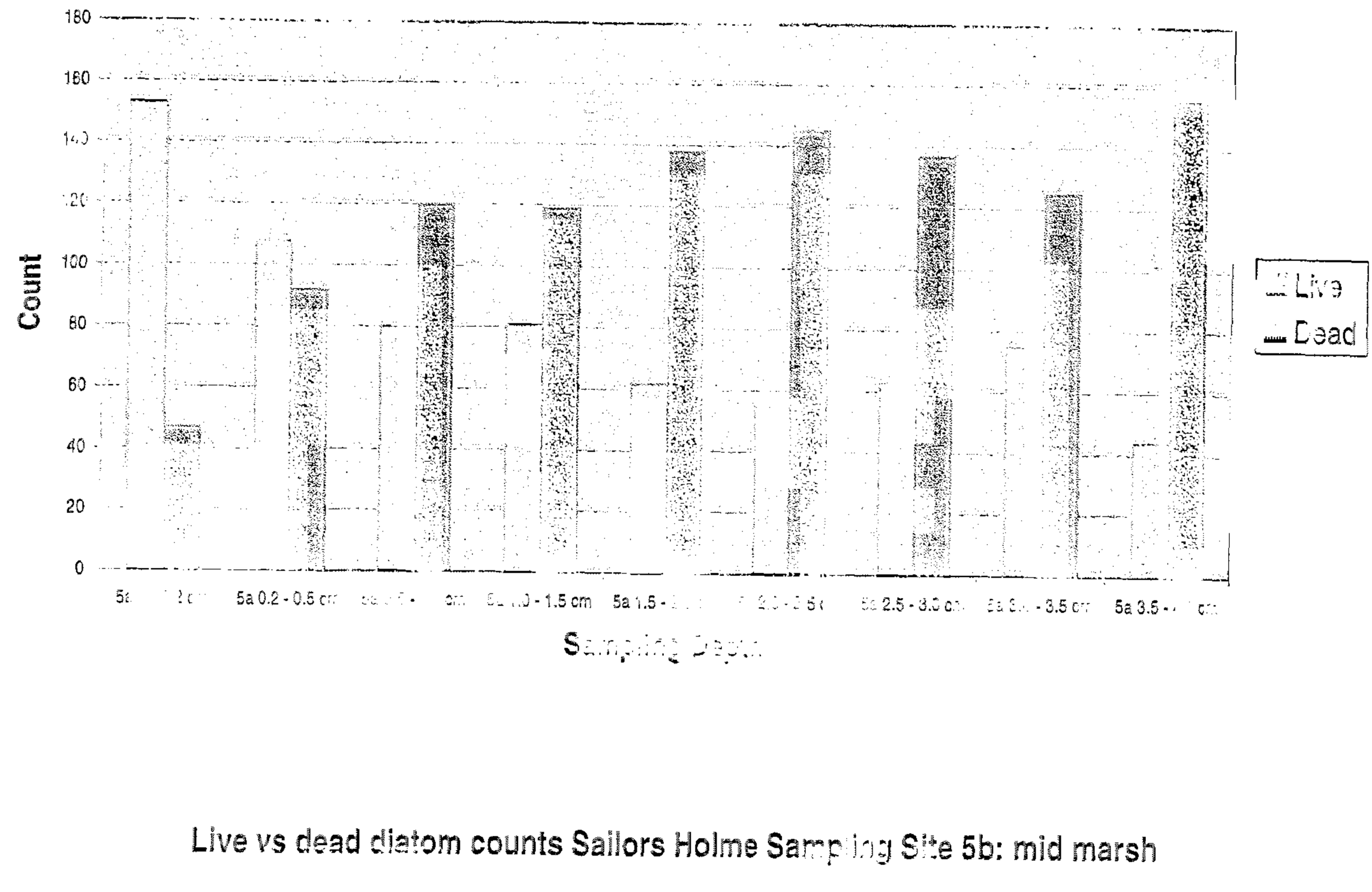


Figure 4.2 Live Dead Counts Sampling Point 5, mid marsh

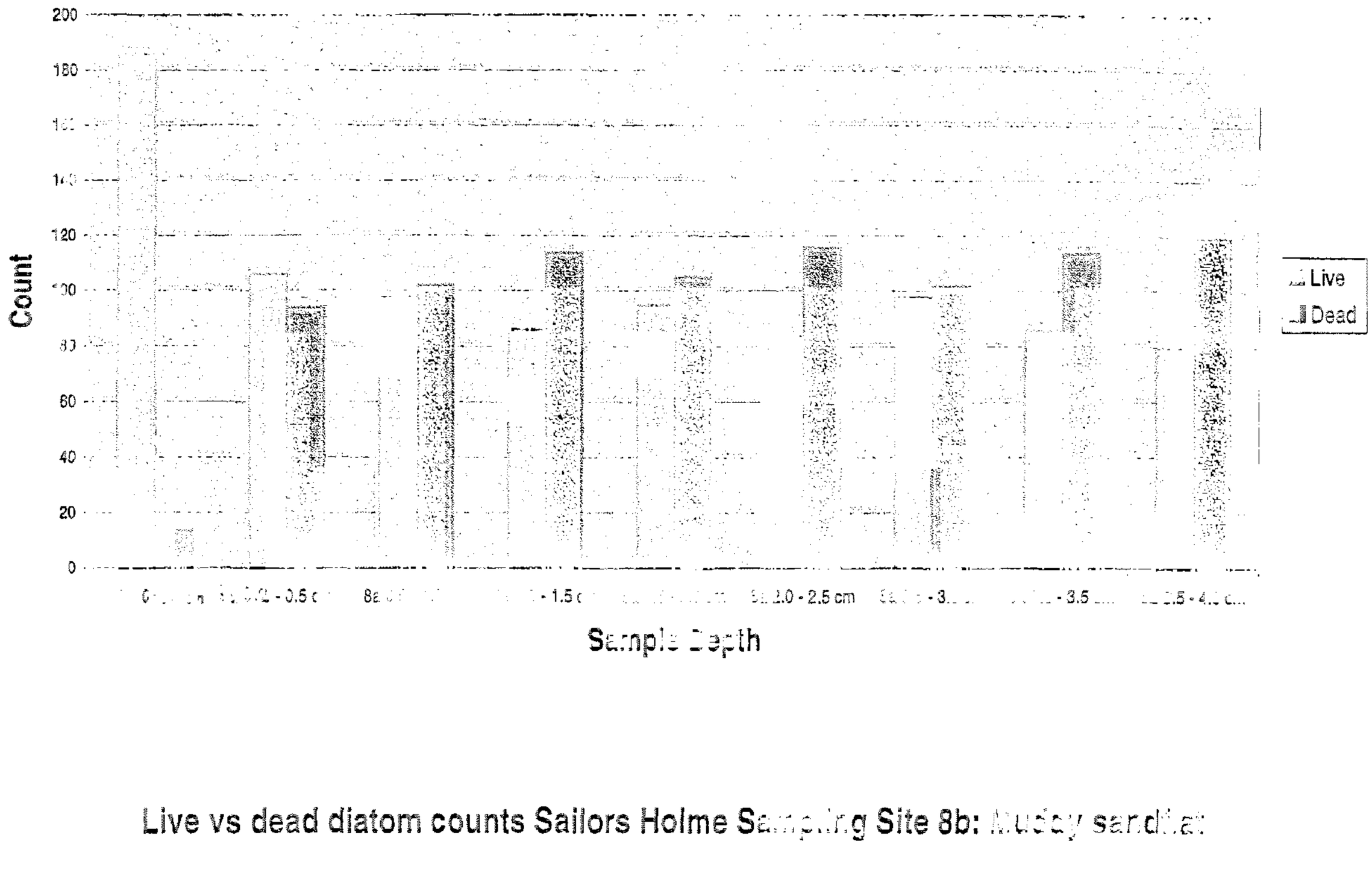


Figure 4.3 Live Dead Counts Sampling Point 8

intertidal mudflats. The high marsh samples also displayed the quickest rise in the proportion of dead diatoms below the 0 – 2 mm layer. This may be in part due to the previous explanations, but it is also possible that the drier, firmer sediment led to less surface sediment being dragged down with the corer and hence less contamination of the lower layers.

The muddy sandflat samples contain the highest proportion of live diatoms throughout. This is likely to be due to the higher productivity of the environment and an increase in motile diatoms in the looser wetter sediment. Furthermore, the sandier nature of the sediment leads to more open drainage allowing surficial pore water, potentially containing live diatoms, to seep through to the lower layers as the core is taken and sectioned.

The mid marsh cores show the greatest intra-site variation, but in general fall between the higher marsh cores and muddy sandflat cores in terms of proportions of live diatoms.

Overall there is a high degree of consistency in the level at which the proportion of dead diatoms becomes greater that that of live cells; for all samples it is at 0.5 – 1.0 cm apart from core 5b from the middle marsh, which is at 1.5 – 2.0 cm.

These results suggest that the 0 – 0.2 mm samples contain such a large proportion of living diatoms that the inclusion of this section would lead to a strong bias towards the living assemblages collected. The 0.2 – 0.5 cm depth would appear to be a better choice of sample in order to obtain the subfossil community with less seasonal overprinting.

In deciding the most suitable sampling depth a number of other factors need to be brought into consideration.

- Sediment mixing
- Different depositional environments
- Proportion of live diatoms in the sample

The final sampling method adopted to remove the top 2 mm of sediment in which the majority of the living diatoms are to be found as demonstrated above. Following this a 5 – 8 cm syringe-core was taken, and sectioned at 5 mm intervals. The sample to be used for analysis was the 0 - 0.5 cm sample from the core (0.2 - 0.7 mm depth from the sediment).

4.4 Field methods

4.4.1 Sediment sample collection

At each Site a straight transect was located from as near to HAT as the natural transition reached, depending on the presence or absence of artificial sea embankments or walls, down to either the lowest point exposed by the tides at the time of sampling, or the lowest accessible point. At sites with embankments or sea walls the transect line was chosen to avoid, where possible, any erosional features at the foot of the artificial structure. The sampling station was set up above HAT wherever possible, such as on top of a sea embankment, where present. The elevation along the transect was determined according to the surveying method described below.

Along the transect between three and eight Sampling Points were chosen depending on the variety of intertidal habitats present and the gradient of the Sampling Site. To ensure each Sampling Point was representative of the habitat being sampled, the exact location of each Sampling Point was chosen to be central, in terms of area and elevation, within that habitat. Obvious erosional features were avoided as the surface sediment exposed would not represent a modern depositional environment. At each Sampling Point two repeat cores were taken using the hand-held syringe corer described above. At the point where each core was to be taken, the top 2 mm of sediment were scraped off carefully using a spatula and bagged. The core was then taken and sectioned immediately into 5mm sections to a depth of up to 8 cm .

A bulk sample was also taken at each sampling point. A small trowel was used to remove approximately 5 cm^2 of sediment to a depth of 1 cm. This sample was retained for salinity, grain size and organic content analysis. Great care was taken to ensure that each core and the bulk sample were taken from sediment at the same elevation and from the same microenvironment.

These sites were each sampled once between December 1997 and September 1998.

4.4.2 Surveying and elevation data

Each Sampling Point was surveyed from a base station. The surveying base station was positioned such that the full transect to be surveyed was visible. Two or more fixed points that could be easily identified on a map were surveyed in order to fix the absolute position of the transect. The elevation of the transect was then fixed to Ordnance Datum using a Sokkia level and staff between one of the fixing points and the nearest OD bench mark.

The OD heights of each Sample were then converted to distance above or below ML at each site. Tidal height data was obtained from the Admiralty Tide Tables for 1998 (Admiralty, 1997). In order to standardise the elevation of each Sample relative to ML a standardised water-level index (SWLI) equation published by Zong and Horton (1999) was used. The equation used is as follows:

$$X_{ab} = [((A_{ab} - ML_b)/(MHWS_b - ML_b) \times 100)]$$

Where (after Zong and Horton, 1999) :

- X_{ab} is the SWLI of the sample *a* at site *b*;
- A_{ab} is the measured altitude (m OD) of the sample *a* at site *b*;
- ML_b is the mean tide-level (m OD) at site *b*;
- $MHWS_b$ is the mean high water spring tide at site *b*.

Zong and Horton (1999) add a constant of 200 on the final SWLI figure to ensure all values were positive. For the purpose of this study this was not deemed necessary hence the range of the SWLI is from –1 to +1 with a value of 0 equating to ML, -1 to MLWS and +1 to MHWS. So as not to create confusion between the published SWLI index equation which requires the addition of the constant and the standardised water levels calculated here without the constant, the latter are referred to from here on in as the normalised tidal height of a Sample.

Gehrels (2000) argues the case for converting normalised height measurements into a measure of normalised flooding duration, the latter being the ecological parameter that benthic intertidal species are responding to rather than elevation, which on its own has no ecological meaning. The graph of normalised tidal height against normalised flooding time in Gehrels

(2000) shows a roughly linear relationship over the majority, becoming increasingly non-linear on the upper marsh surface where the time of sub-aerial exposure is very sensitive to small change in height (Gehrels, 2000). Gehrels (2000) goes on to develop a predictive regression model for both normalised elevation and flooding frequency and the latter was found to perform slightly better, but these cannot be directly compared to the model developed in this study as Gehrels (2000) employs *foraminifera* and not diatoms as the palaeoenvironmental indicator.

The roughly linear relationship, shown in Gehrels's (2000) model, over most of the intertidal gradient and the fact that flooding frequency data is calculated directly from the tidal height data suggests that normalised tidal height is an adequate proxy for the ecological variable of exposure. However, Gehrels (2000) results do engender caution in the interpretation of results at the highest intertidal elevations.

4.4.2.1 Sources of error

There are a number of potential sources of error associated with the survey and elevation data that should be taken into account when interpreting results. Errors in levelling are estimated, from trials, to be +/- 0.1 m. In addition the use of bench marks to fix the elevation along a transect to OD can introduce error as some bench marks may have altered slightly in elevation since the exact height of the bench mark was determined and published, and there may be small inherent errors in the original bench mark height due to the length of the survey line from Newlyn (Shennan, 1986). Shennan (1986) estimates that the error in benchmark values in England and Wales is in the region of +/- 0.15 m, and +/- 0.2 m in Scotland.

A further possible source of error relates to the tidal wave. The shape of the tidal wave can change as it moves up an estuary, altering the timing and duration of the flood and ebb tide. This can introduce an additional source of error for sites located away from the mouth of an estuary. Finally, Sampling Sites are located at differing distances from the nearest port for which tidal height data is given in the Admiralty Tide Tables for 1998 (Admiralty, 1997). Those located furthest way will have the highest degree of error associated with the tidal height data applied for the Site.

4.4.3 Vegetation and habitat

At each sampling site a $1m^2$ quadrat was placed and vegetation recorded. There are a number of methods in the literature for the estimation of vegetation cover (see Kent and Coker, 1994; Kershaw and Looney, 1983). Of these, the well-recognised Braun-Blanquet cover scale (first described by Braun-Blanquet in 1927) was used as it combines simplicity and speed with conveyance of main vegetation information. The scale, shown in Table 4.1, refers to the ground coverage of the above-ground parts, as estimates by eye. The vegetation data was used to categorise floral community according to the National Vegetation Classification (NVC) system using Rowell (2000). The NVC of Samples from vegetated habitats is given in Appendix 1.

Table 4.1 The Braun-Blanquet Vegetation Cover Scale

Value	Coverage
+	Less than 1% cover
1	1-5% cover
2	6-25% cover
3	26-50% cover
4	51-100% cover
5	76-100% cover

Each Sampling Point was also classified in terms of its habitat. In order to ensure habitat categorisation was carried out consistently an environmental classification was developed and each Sampling Point assigned to a habitat type. The classification used is shown in Table 4.2. The division of habitats from the intertidal flats is based on sediment properties with three main types identified: sandflat, muddy sandflat and mudflat. Saltmarsh categories were primarily assigned on the basis of the vegetation community according to Rodwell (2000) who distinguished between high,

Table 4.2 Environmental classifications used to categorise the habitat-types of each Sample

Habitat	Abbreviation
Sandflat	SF
Muddy sandflat	SFM
Mudflat	MF
Creek	CR
Dry pan	PAN DRY
Wet pan	PAN WET
Low/pioneer saltmarsh	SML
Mid saltmarsh	SMM
High saltmarsh	SMH
Back of saltmarsh	SMB
Phragmites australis bed	PH

middle and low saltmarsh vegetation communities. In addition, field observations on the position along the intertidal gradient (where this could be ascertained) were also employed, based on Long and Mason's (1983) description of saltmarsh development in relation to the tidal gradient. Thus, for example, the definition 'high saltmarsh' was only assigned to Sampling Points around and above MHWS. The presence of even sparse coverage of pioneer vegetation species, such as *Salicornia* spp., was used as a criterion for categorisation as low/pioneer saltmarsh, according to descriptions of the low saltmarsh communities given by Rodwell (2000). Within this study the terms low and pioneer saltmarsh are taken as being synonymous. The category of back saltmarsh is reserved for transitional vegetation communities at the landward extreme of the intertidal environment, above MHWS. Back saltmarsh habitats are distinct from high saltmarsh habitats, partly in terms of elevation, but also by sediment and vegetation characteristics. Here, the back saltmarsh habitat is taken to be one where the substrate is peaty in nature and the vegetation is dominated by more oligohaline marsh species such as *Juncus maritimus* or *Elymus* spp.

4.5 Laboratory methods

4.5.1 Diatom preparation and counting

Once collected the 0.5 cm samples were prepared for diatom analysis from each Sampling Point. Diatom preparation followed Battarbee (1986) with some minor alterations to the method following Renberg (1990) and Hinchey (1994). Instead of centrifuging the samples to clean them, the samples were cleaned by suspending in distilled water and leaving to settle over night. The washing water was then decanted and the procedure repeated five times. The washing was done this way in order to minimise breakage of diatoms that might occur in the centrifuge. Also, a few drops of ammonia were added to the second to last wash; this helped to retain clay particles in suspension, which could then be removed with the washing water.

Diatom slides were counted using a Leitz Laborlux microscope at 1000x magnification. Five hundred diatoms were counted from each slide and identification was carried to species level or lower where possible. Due to the fragmented nature of the taxonomic literature for estuarine and coastal diatoms it was not possible to follow one reference. Instead the following references were used for identification: Archibald (1983); Campeau *et al.* (1999); Cleve-Euler (1951); Hasle and Syvertsen (1996); Hendy (1954); Hustedt (1959); Krammer and Lange-Bertalot (1986-1991); Pankow (1976); Snoeijs's 'Intecalibration and Distribution of Diatom Species in the Baltic Sea' series volumes I to V (Snoeijs, 1993; Snoeijs and Vilbaste, 1994; Snoeijs and Potapova, 1995; Snoeijs and Kasperoviciene, 1996; Snoeijs and Balashova, 1998); Van der Werff and Hulls (1976); Witkowski (1994) and Witkowski *et al.* (2000).

Because of the problem of the fragmented literature and confusion over the splitting and lumping of a many species, each new species encountered during the counting was photographed and reproduced at x1500 magnification. Small taxa were also reproduced at x3000 magnification. In this way a comprehensive iconography of all species counted was created in order to ensure consistency in identification. A list of all species and their authorities are given in Appendix 2. Authorities are only cited in the text where reference is made to a taxon that is not identified in the diatom dataset (and hence not listed in Appendix 2).

With more difficult taxa, repeat pictures and measurements were taken to get a clearer picture of the morphology of the taxon in question. A significant number of diatoms were identified in new coastal and marine floras by Witkowski (1994) and Witkowski *et al.* (2000) as newly described species. This is indicative of, until recently, the lack of comprehensive floras addressing coastal and marine diatoms and the need for more descriptive taxonomic work in this field, which Witkowski *et al.* (2000) is beginning to address. It is therefore not surprising that 24 taxa could not be identified from the existing literature. Unidentified taxa occurring at a maximum abundance of >2% are listed in Appendix 8 along with morphological descriptions.

4.5.1.1 Problem taxa

In addition to unidentified taxa, some taxa are particularly difficult to place within a specific category. These include taxa that are identified in the literature but which appear to exhibit a continuum of morphological types between published subspecies or species in a genera. The decision of whether to 'lump' morphotypes together under one specific name, or to split them into different species or subspecies should be guided by observations on the ecological distribution of these taxa during diatom counting and analysis.

Three taxonomic groups presented such difficulties in the process of diatom identification and have been grouped together under the title of a species complex. Authorities for individual species and subspecies identified within these complexes are given in Appendix 2. These species complexes include the:

- *Achnanthes delicatula* complex;
- *Navicula digitoradiata* complex;
- *Navicula salinicola* complex.

Achnanthes delicatula complex

The *Achnanthes delicatula* complex is discussed in Krammer and Lange-Bertalot (1991). This group of species exhibits a wide variety in morphotypes that can appear to represent a continuum, making subspecies level identification difficult. However, there are a number of commonly identified subspecies that are particularly distinctive, such as *Achnanthes delicatula* subsp. *hauckiana*. Krammer and Lange-Bertalot (1991) list a number of subspecies

within the complex, including *Achnanthes delicatula* subsp. *delicatula*, *Achnanthes delicatula* subsp. *engelbrechtii*, *Achnanthes delicatula* subsp. *hauckiana* and *Achnanthes delicatula* subsp. *septentrionalis*. Taxa from the *Achnanthes delicatula* complex were identified to these subspecies levels according to the morphological definitions given by Krammer and Lange-Bertalot (1991). However, there were a number of taxa encountered that were clearly part of the *Achnanthes delicatula* complex, but did not fit within morphological definitions given by Krammer and Lange-Bertalot (1991) or any of the other floras consulted (see section 4.5.1 above) for particular subspecies. Two distinct types were identified: a small *Achnanthes delicatula* species that resembles *Achnanthes delicatula* subsp. *delicatula* in all but its size; and a further subspecies that appears to fall between the definitions for *Achnanthes delicatula* subsp. *engelbrechtii* and *Achnanthes delicatula* subsp. *hauckiana*. These are identified consistently throughout this study as *Achnanthes delicatula* (small) and *Achnanthes delicatula* aff. *engelbrechtii*.

Navicula digitoradiata complex

Navicula digitoradiata is a common component of the intertidal saltmarsh community and is found frequently throughout this study. This complex shares a number of features with *Navicula cincta* but is distinguished by its distinctive striae arrangement. It has a large size range and many of the floras listed in section 4.5.1 identify a number of subspecies based on size, striae density and central area variations. A further species type that falls within the morphological complex is described by Lange Bertalot (1993) as *Navicula microdigitoradiata* (formerly *Navicula cincta* fo. *minima*, Van Herff, 1805). Three taxa from this complex were identified in this study based on distinctive morphological variations and differences in ecological distributions. These are *Navicula digitoradiata*, *Navicula digitoradiata* var. *minima* and *Navicula microdigitoradiata*.

Navicula salinicola complex

A number of taxa were encountered that appeared to belong with either *Navicula incertata* (synonyms *Navicula sydowii* (Cholnoky) and *Navicula incerta* (Ehrenberg)) or *Navicula salinicola* although they appear in Krammer and Lange-Bertalot (1986) as separate taxa. These small naviculoid species are described rather inconsistently in the literature with varying upper and lower limits for measurable morphological parameters (see Archibald, 1983; Hartley, 1996; Hustedt, 1939; Krammer and Lange-Bertalot, 1986; Snoeijs, 1998; Witkowski; 1994). Furthermore, the definitions given for these species overlap, making

separation of the taxa arbitrary for many specimens. Witkowski *et al.* (2000) give *Navicula incertata* as a synonym for *Navicula salinicola* and because the full morphological variation within these species is found in a number of Samples, indicating no ecological basis for splitting the taxa, this synonym is adopted here with all taxa fitting the definition of *Navicula incertata* and *Navicula salinicola* identified as *Navicula salinicola*.

4.5.2 Salinity

Salinity measurements were carried out on the bulk samples from each sampling site using a 4010 Conductivity meter calibrated with a 1,413 µS/cm standard solution. A known volume and weight of sediment was added to a 100 ml beaker and distilled water added to make a wet sediment paste; it is possible to determine the conductivity of the sediment or pore-water alone (see Bower, 1965), but for the purposes of this study it was felt that the salinity measurement was better taken from a wet sediment paste, as this would more realistically reflect the salinity of the environment that the diatoms inhabited. The distilled water was added from a volumetric flask in order to be able to record the volume of water added to the sediment. The conductivity of the wet sediment paste was then measured. This conductivity measurement was converted to a measurement of salinity results categorised in terms of salinity classes used by Underwood *et al.* The salinity categories used are shown in Table 4.3.

Table 4.3 Salinity categories assigned to sediment samples, after Underwood et al. (1998)

Category	Salinity Range
Euhaline	> 30 ppt
Polyhaline	18-30 ppt
Mesohaline	5-18 ppt
Oligohaline	0.5-5 ppt
True Fresh	<0.5 ppt

Measuring the salinity of the wet sediment paste from the sampling location may differ from the salinity of the tidal water at any one time due to effects of rain, evaporation, stage of the tidal cycle and seasons (Underwood, 1994) and these constant fluctuations introduce an

element of error in terms of representivity into a single spot measurement. However, it is the local salinity that the diatom assemblage sampled is responding to rather than the open water of the estuary (see Sherrod, 1999; Underwood, 1994), and, although there is the question of representivity of the single wet sediment past salinity sample, it is considered, here, better to work with this degree of error than use a salinity measurement that is known not to relate to the diatom assemblage composition.

Where available, salinity data was also obtained from the Environment Agency and the Scottish Environment Protection Agency. However, as salinity monitoring of estuaries does not form part of either agencies core monitoring programme there is an enormous variety in the amount and applicability of data available with a number of sites having no other salinity data available. It was therefore not possible to develop a mean salinity value for each of the Sites. However, a mean salinity value, based on estuarine open water salinity, would not necessarily bear much relationship to the salinity profile across the intertidal environment. Instead, the salinity class assigned to each sample from the analysis of the wet sediment paste was compared to the class that the sample would fall into from the Agency data provided. All samples with additional data available fell into the same salinity classes so it was felt that the results from this study could be taken forward into the analysis with confidence.

4.5.3 Grain size

Grain size analysis was carried out on the bulk samples from each sampling site. Particle size analysis was carried out with an electrical sensing zone method using a Coulter Granulometer Particle Size Counter (see Goudie *et al.*, (1998) for details). A weighed sample of disaggregated sediment was prepared and sieved through a 2.00 mm sieve. The organic matter was then removed from the samples using hydrogen peroxide. Approximately 0.5 g of the sediment was placed in a 50 ml tube and 20 ml of 20% hydrogen peroxide added. The tubes were then covered with aluminium foil and placed in a boiling water bath for two hours. After this time the samples were checked. If any organic material remained more hydrogen peroxide was added and the tubes returned to the water bath for a further two hours. This was repeated until all the organic material had been oxidised. The samples were then run through the Coulter Counter (for details see Goudie, 1998).

4.5.4 Loss on Ignition

The organic content of the bulk samples for each sampling site was determined through percentage loss on ignition following Dean (1974).

4.6 Data analysis

4.6.1 Descriptive analysis

The data analysis is prefaced with a broad overview of the distribution of samples geographically and by habitat type followed by a descriptive analysis of the overall diatom flora and sites without diatoms. Species abundance and N_2 diversity are also calculated. The N_2 diversity index is a useful measure of species distributions given either the effective number of taxa per Sample (N_2 for a Sample), or the effective number of occurrences for each taxa (N_2 for taxa). As such it is less sensitive to sample size and taxonomic resolution than the number of taxa in a sample or the number of occurrences of a taxon (Hill, 1973). The distribution of diatom assemblages and species within and between Sites is analysed in a descriptive manner with plots of the more abundant species at each Site and within each habitat.

4.6.2 Cluster analysis of the diatom assemblages

By excluding from analysis rare taxa with an abundance less than 2% in any sample the number of taxa is reduced from 466 to 183. This is still, however a very large number of species from which to glean patterns and ecological preferences, especially given the generally noisy nature of coastal diatom assemblages due to taphonomic overprinting. To simplify the diatom data a classification of samples is performed using cluster analysis. Cluster analysis begins with no assumptions of pre-existing groupings in the data and is therefore termed unsupervised pattern recognition. There are a number of methods for performing cluster analysis and these are described and reviewed by several of authors including (Everitt and Dunn, 1991 and van Tongeren, 1987). The method applied here is a Two-way Indicator Species Analysis (TWINSPAN; Hill, 1979), being a particularly useful method for large noisy datasets (Gauch and Whittaker, 1981). This is a divisive hierarchical method that starts with

one large group and performs successive divisions into smaller groups nested within the larger groups already delineated. TWINSPAN splits the dataset by performing repeated ordination analysis and splitting the group at the centre of the major axis, i.e. the axis that explains the largest amount of variation within the dataset.

The reliability of this method does depend on how well the correspondence analysis extracts axes that have ecological meaning, so *a priori* knowledge of the dataset is very important in interpreting the TWINSPAN output, hence the need to carry out a full descriptive analysis before embarking on the cluster analysis.

Once the groups have been extracted from the TWINSPAN output their distribution within the other environmental variables is examined.

4.6.3 Canonical Correspondence analysis

Following the exploration of diatom environment relationship through the TWINSPAN analysis the strength of the relationship between the diatoms and environmental variables is quantified and explored with the aid of Canonical Correspondance Analysis (CCA). This is an ordination technique that extracts environmental gradients from the diatom dataset. The use of CCA requires a unimodal abundance pattern within the diatom data. Exploratory analysis of the environment variables and diatom data indicated that transformations were not needed before quantification of the diatom environment relationships could be undertaken.

Variance partitioning is undertaken by performing a series of CCAs and partial CCAs to identify a list of significant environmental variables in terms of explaining variance within the diatom dataset. An unrestricted Mote Carlo permutation procedure is used to test the significance of each variable (999 permutations). Variance partitioning quantifies the amount of variation within the diatom dataset that each environmental variable explains both uniquely and as co-variables. An environmental variable must, independently, explain a significant degree of the variance within the diatom data to be utilised in a predictive model (Birks, 1995). CCAs and partial CCAs were performed using the program CANONCO version 4 (Ter Braak and Smilauer, 1998).

To reduce the complexity of the dataset environmental variables are amalgamated into groups representing the main environmental gradients in the dataset. CCA with forward selection was then used to select and test the significance of the environmental variables to represent these gradients. The environmental variable groupings used are:

- Exposure: Normalised tidal height;
- Sediment properties: grain size parameters and LOI;
- Salinity: absolute values and salinity classes;
- Habitat: nominal variables representing the main habitat types listed in Table 4.3,
- Region: nominal variables representing the spatial location of the sites listed in Table 2.3)

CCA results are presented as bi-plots that map the environmental variables along the gradients extracted from the floristic data.

4.6.4 Individual diatom species distributions over the tidal gradient

In addition to the community-wide analysis of the diatom *assemblages* using CCA, four response models are used to test the significance of individual species distribution along the normalised tidal height gradient. The four models used are: null (no significant relationship), logistic regression (a linear relationship), Quadratic (A Gaussian, or Quadratic, response curve) and General Additive Model (GAM) (Birks *et al.*, 1998). The GAM fits a smooth logistic response function through the data and allows fitting of more flexible response functions including monotonic, unimodal or non-symmetric response curves. These models increase in complexity so the principal of parsimony is applied, choosing the simplest model that shows a significant relationship to the distribution of the diatom species along the tidal gradient. Only when a more complex model explains a significantly greater degree of the distribution in the data than a simpler model is this model applied to the data. The fit of a model is significant where a P value is returned greater than 0.001. Species optima and tolerance along the tidal gradient are calculated using weighed averaging optima.

4.6.5 Predictive model development

A weighted average (WA) transfer function is developed to calibrate normalised tidal height, based on the 183 species with an abundance greater than 2%, using the CALIBRATE program (Juggins and Ter Braak, 1998). This is a method by which an environmental variable is calibrated as a function of the species community composition. This is a more robust method than reliance on the autecology of individual indicator species.

WA is used as this is suitable for species that respond unimodally to an environmental variable (Birks *et al.*, 1990). The species are not uniformly distributed along the tidal height gradient and WA is fairly robust is these instances. It is likely that WA provides the most appropriate regression technique with which to predict tidal height from this training dataset, but other regression methods are also used to test whether or not they improve on the WA predictions. The variety of prediction methods available along with numerous examples of their application is reviewed by Birks (1998). The WA partial least squares (WA-PLS) regression method is tested, although this method is generally more suitable for less noisy data (Ter Braak and Juggins, 1993).

Samples that had a poor fit to tidal height were identified as outliers (three in total, discussed in section 6.4) and deleted from the model where the standard residual was greater than 2.5, and therefore in the 99% extreme of the distribution. Model performance is assessed in terms of apparent and jack-knifed predictions and the associated root mean squared error (RMSE), root mean squared error of prediction (RMSEP, or $RMSE_{jack}$) and maximum bias. The apparent RMSE is a measure of the difference between the observed and predicted values in the model where the Sample for which the prediction is generated is included in the model. The $RMSE_{jack}$ is a measure of the difference between the observed and predicted values for a Sample where that Sample is omitted form the model and its position along the environmental gradient is reconstruction from the remaining training set; this method is known as jack-knifing (Ter Braak and Juggins, 1993). The maximum bias returns the largest difference measured between the mean observed and predicted values and the value given is taken from 10 values along the environmental gradient (Birks, 1998).

A series of predictive models are also developed for individual regions and groups of regions.

A model is also developed for predicting habitat from the diatom data. This is done using an analogue-matching technique, matching each 'unknown' sample to the database using a squared chord distance coefficient (Overpeck, 1985).

CHAPTER 5

DIATOM-ENVIRONMENT RELATIONSHIPS

5.1 Introduction

This chapter explores the relationships between diatom subfossil assemblages, and the environmental variables of habitat, salinity, elevation, geographical location and sediment properties of grain size and organic content (loss on ignition). Firstly an overview of broad properties of the dataset is given. This is followed by a description of the diatom flora found at different sampling Sites and in different habitats. Cluster analysis is then carried out on the diatom species using TWINSPAN to identify groupings in the diatom data. Relationships between the diatom TWINSPAN groups and salinity, habitat and elevation are explored in an attempt to classify the environmental affinities of each of the diatom groups delineated in the cluster analysis.

Throughout the description and analysis of results elevation is used is terms of the tidal gradient, hence a Sample referred to as having a high elevation means that the Site has an elevation at the higher end of the tidal gradient, and vice versa. The term intertidal flat is used collectively to refer to the mudflat, muddy sandflat and sandflat habitats.

5.2 The Sampling Sites: general characteristics

5.2.1 Distribution of Samples over intertidal habitats

Chapter three gives a description of the Sites chosen for sampling, along with an explanation of the Site selection process. The actual individual Samples collected span the full range of habitats set out in the environmental classification detailed in section 4.4.3. The distribution of Samples across these habitats in macro-, meso- and microtidal environments is displayed in Table 5.1. In keeping with the distribution of estuaries selected for sampling, the largest number of Samples occurs in macrotidal environments, the dominant tidal range type in Britain. Mudflats, sandflats, low and high saltmarsh make up the majority of the Samples

reflecting the distinctive nature of these environments. All other habitats listed are either transitional to some degree or hydrodynamic features of the intertidal environment (creeks and pans). The only microtidal Samples come from the only microtidal Site, Poole Harbour, with only mudflat and *Phragmites australis* habitats found at the Site. *Phragmites australis* beds are also sampled at Bridgewater Bay, and Blacktoft Sands, both macrotidal environments. A number of pan and creek Samples are included in the training dataset for completeness to check for any distinctive assemblage associated with these habitats, although their distribution across much of the tidal range above ML may obscure any habitat relationships. The full range of Sample properties are contained in Appendix 7.

Table 5.1 Numbers of Samples collected by habitat in macro- meso- and microtidal estuaries

Habitat	Macrotidal	Mesotidal	Microtidal	Total
Sandflat (SF)	11	2		13
Muddy sandflat (SFM)	5	2		7
Mudflat (MF)	18	7	2	27
Creek (CR)	3	4		7
Pan – dry (PA DRY)		2		2
Pan – wet (PA WET)	5			5
Low/pioneer saltmarsh (SML)	12	7		19
Mid saltmarsh (SMM)	9	2		11
High saltmarsh (SMH)	12	4		16
Back of saltmarsh (SMB)	3	1		4
Phragmites australis bed (PH)	3		2	5
Total	81	31	4	116

5.2.2 Samples with badly preserved diatom assemblages

Of the 127 Samples analysed for diatom content, 11 did not contain diatoms, or the diatom remains were too degraded and sparse to allow identification or quantification of the assemblage. The distribution of the 11 Samples without diatoms is shown in Table 5.2. Only five estuaries had Samples collected that did not contain diatoms, the Humber, Severn,

Mawddach, North Norfolk Coast and Solway Firth. The lack of diatoms in 4 sandflat Samples with a very high proportion of sand is not surprising as this habitat is frequently scoured by the tide removing much of the diatom flora (De Jonge 1985). The Mawddach estuary Sample without diatoms was taken from the base of a shallow, sandy creek and the Solway sandflat Sample came from below MLWN near the main Solway channel. The constant ebb and flow of the tide through the Mawddach creek and the Solway channel would amplify the phenomena already described for sandy sediments. The 3 Severn sandflat Samples are all taken from the Site at Arlingham. This Site is only a few kilometres short of the tidal head of the Severn estuary on a large meander in the river. The Samples were taken from the inside depositional bank where a fine film of silt accumulate. This bank is covered by every tide and the sandy nature of the sediment means that the bank is likely to be shifting constantly with little chance of preservation of diatoms.

The 3 Samples on the North Norfolk coast without diatoms were all from Burnham and include Samples from low, high and back saltmarsh habitats. When Burnham was sampled the tide was in the neap section of the tidal cycle and none of these habitats had been inundated by the tide for some time, the sediment surface was desiccated with a film of salt deposit on the surface. This desiccation, cracking up the top layers of sediment, is also likely to be the cause of the sparse, highly degraded diatom Samples recovered from these three points. This effect of desiccation also accounts for the lack of diatoms in the high saltmarsh Sample from the Humber at Blacktoft sands. The Sample came from a high saltmarsh habitat dominated by a relatively open cover of *Scirpus maritimus*, National Vegetation Classification community S21, *Scirpus maritimus* swamp. A classification of all vegetated Sample habitats according to the National Vegetation Classification (Rodwell, Ed, 2000) is given in Appendix 1. This habitat occurred between MHWN and MHWS and was, again, sampled during the neap phase of the tidal cycle leaving the exposed sediment dry and cracked. Diatoms were recovered from the *Phragmites australis* beds at Blacktoft Sands high up the tidal range around MHWS, but the tall cover of reeds kept the surface sediment moist, avoiding desiccation and consequent destruction of the living and subfossil diatom flora.

Two Samples from Bridgewater Bay in the Severn estuary did not contain identifiable diatom remains. These came from the low saltmarsh and the high saltmarsh. The low saltmarsh Sample was categorised as such because of the point along the intertidal gradient and the sparse coverage of Spartina in the $1m^2$ quadrat around the Sample. Unlike most Samples from a similar point along the tidal gradient, the sediment was sandy, forming a sandy band

between the mid marsh and the mudflats. The lack of diatoms in this Sample is therefore likely to be caused by the properties of sandy intertidal environments discussed above. The high marsh Sample is harder to explain, but may be due to similar factors described for Burnham and Blacktoft above.

All analysis from this point on is based on the 116 Samples with diatom counts.

Table 5.2 Distribution of Samples with no diatoms recovered

Habitat	Estuary	Number of Samples
Sandflat (SF)	Severn	3
Sandflat (SF)	Solway Firth	1
Creek (CR)	Mawddach	1
Low/Pioneer Saltmarsh (SML)	North Norfolk Coast	1
Low/Pioneer Saltmarsh (SML)	Severn	1
High Saltmarsh (SMH)	Humber	1
High Saltmarsh (SMH)	North Norfolk Coast	1
High Saltmarsh (SMH)	Severn	1
Back of Saltmarsh (SMB)	North Norfolk Coast	1
Total		11

5.3 Diatom species distributions

Before embarking on diatom species and assemblage analysis in any detail it is worth reiterating the fact that distributions of individual species are indicative of subfossil assemblages distributions and as such cannot be expected to follow exactly the distribution of their live counterparts. A large body of literature exists on the distribution of living diatoms species and composition of living assemblages in coastal environments (see Chapter Two) and whilst this can be used for comparative purposes the subfossil distributions will always be expected to be broader in terms of environmental gradient distributions due to the effect of taphonomic processes.

5.3.1 Overall species diversity and abundance

A total of 466 taxa were identified from the 116 Samples analysed for diatom content. Of these 116 Samples, the mean number of taxa identified per Sample was 64, with a total range from 32 on the sandflats at Skyreburn Bay (Sample SB4) to 108 on the Exe mudflats (Samples EX4). The number of taxa encountered in a Sample can be expressed using the N_2 diversity index (see section 4.6.5). Table 5.3 summarises the frequency distribution of N_2 Sample diversity and reveals a symmetrical pattern with the majority of Sites falling into the 10 – 15 N_2 diversity class with a symmetrical tail off above and below. The vast majority of Samples have a relatively high diversity and all are above an N_2 value of 2, considered as species poor by Allott and Flower (1997) in reference to diatom Samples from Welsh lakes. Diatom diversity in lakes is often high due to the numerous niche environments, but this dataset indicates that coastal diatom diversity is, on average, higher, due to the additional sources of allochthonous species. An N_2 diversity value less than 5 could be considered to represent a species poor Sample in this dataset. All Samples falling below an N_2 diversity value of 5 come from either a sandflat environment or high elevation environments (including high saltmarsh, high elevation pans and *Phragmites australis* beds). This reflects the harsh environmental conditions which need to be overcome for diatoms to survive in these habitats; sandflats in terms of their instability and high tidal elevation habitats due to their infrequent inundations and resultant broad fluctuations in salinity and sediment water content.

Table 5.3 Frequency distribution of N_2 Sample diversity for intertidal Samples

N_2 diversity	< 5	> 5 - < 10	> 10 - <15	> 15 - < 20	> 20
Number of Samples	13	27	42	27	7

Over half the taxa encountered had a maximum abundance of less than 1.5% revealing a very large number of rare taxa. This is not surprising, as each flood tide will deposit allochthonous taxa from the estuarine plankton and benthos from other intertidal environments whilst the river flow will bring freshwater species into the intertidal environment thus creating a large diversity of species over and above the more abundant autochthonous species. The number of species with a maximum abundance greater than 2% is 183, greater that 5%, 94 species. All

diatom taxa encountered with an abundance greater than 2% are listed in Appendix 2. The diatom taxa with the 20 highest N_2 diversity values and the 20 highest maximum abundances are shown in Tables 5.4 and 5.5 respectively, for comparative purposes. The two lists only share six species in common and these are *Rhaphoneis minutissima*, *Navicula perminuta*, *Cymatosira belgica*, *Navicula phyllepta*, *Achnanthes delicatula subsp. hauckiana* and *Navicula gregaria*. *Navicula gregaria*, appears to be a highly adaptable species occurring in a wide variety of habitats, although more commonly found on the vegetated saltmarsh than on the bare intertidal flats and is a species also commonly found in rivers and lakes. *Navicula phyllepta* is another taxa with wide salinity tolerances variously categorised as euryhaline (Van de Werff and Hulls, 1976) and freshwater (Hartley, 1996) and is frequently recorded as a common species in a wide variety of coastal diatom studies (e.g. Juggins 1992). The remaining four taxa listed, with both a high N_2 diversity and a high maximum abundance, are all recorded in the literature as species common on intertidal flats (e.g. Hartley, 1964; Horton, 1997; Vos and De Wolf 1993a). Their abundance in this more mobile, regularly inundated habitat may explain their frequency of occurrence in other intertidal Samples; they are probably forming an important part of the autochthonous flora transported up the tidal gradient by the flood tide.

In examining Tables 5.4 it is clear that there are a number of taxa with relatively high N_2 diversity values, occurring in a large number of Samples, but never at particularly high abundances. These taxa can be described ecologically, in terms of subfossil assemblages, as cosmopolitan but rarely abundant. As well as including a number of well-known intertidal diatoms such as *Delphineis surirella* this group also includes estuarine planktonic forms such as *Paralia sulcata* (this definition is discussed in section 5.3.5), *Thalassionema nitzschiodes* and *Actinocyclus senarius*, and taxa with salinity tolerances at or near freshwater such as *Gyrosigma peisonis* and *Achnanthes minutissima*. Taxa with low N_2 values but high maximum abundances represent species that were infrequently found, but when they were, tended to dominate Samples, possibly because of a high degree of contamination of the subfossil Sample with live taxa. These taxa can be described ecologically, in terms of the fossil assemblages, as being rare but occasionally locally abundant. *Navicula arenaria* is a case in point, occurring in 25 Samples and at maximum abundance less than 1% in 23 of these, but reaching an abundance of 67% in Sample SP3 taken from below ML on the sandflats at Spurn point. The high abundance probably resulting from a high degree of surface diatom contamination in the subfossil Sample due to movement of pore water during sampling in what was a waterlogged sediment surface.

Table 5.4 Diatom taxa with the 20 highest N_2 diversity values

Rank	Taxon Code	Taxon Name	Maximum % Abundance	N_2 diversity
1	RA007A	*Rhaphoneis minutissima*	44.0	64.0
2	NA614A	*Navicula salinicola*	27.0	46.3
3	NA565A	*Navicula perminuta*	34.0	39.0
4	RA002A	*Rhaphoneis amphiceros*	2.0	37.7
5	TL001A	*Thalassionema nitzschioides*	1.8	37.0
6	XXX550	*Amphora* c.f. *delicatissima*	3.2	34.9
7	AT010A	*Actinocyclus senarius*	3.0	34.2
8	CT001A	*Cymatosira belgica*	30.5	34.1
9	DEL01A	*Delphineis surirella*	7.9	33.8
10	NA058A	*Navicula phyllepta*	30.8	33.7
11	PA001A	*Paralia sulcata*	12.4	33.5
12	AC016A	*Achnanthes delicatula* subsp. *hauckiana*	21.1	33.2
13	XXX391	*Nitzschia fontifuga*	12.3	31.2
14	GY021A	*Gyrosigma peisonis*	8.7	30.4
15	NI015A	*Nitzschia dissipata*	10.5	29.4
16	NA023A	*Navicula gregaria*	44.4	28.6
17	AM002A	*Amphora acutiuscula*	7.5	28.1
18	NI008A	*Nitzschia frustulum*	4.3	28.0
19	AC013A	*Achnanthes minutissima*	2.6	27.7
20	XXX643	*Navicula* sp. A	16.0	26.9

Table 5.5 Diatom taxa with the 20 highest maximum abundances

Rank	Taxon Code	Taxon Name	Maximum % Abundance	N_2 diversity
1	NA220A	*Navicula arenaria*	67.6	1.5
2	NA021A	*Navicula cincta*	61.2	18.0
3	NA023A	*Navicula gregaria*	44.4	28.6
4	RA007A	*Rhaphoneis minutissima*	44.0	64.0
5	NA565A	*Navicula perminuta*	34.0	39.1
6	NA058A	*Navicula phyllepta*	30.8	33.7
7	CT001A	*Cymatosira belgica*	30.5	34.1
8	XXX652	*Biremis lucens*	29.0	13.4
9	CO007A	*Cocconeis scutellum*	28.5	8.1
10	NA614A	*Navicula salinicola*	27.0	46.3
11	XXX928	*Navicula microdigitoradiata*	26.8	23.1
12	XXX931	*Navicula germanopolonica*	24.8	17.4
13	NA022A	*Navicula halophila*	22.7	12.5
14	AC016C	*Achnanthes delicatula* subsp. *hauckiana*	21.1	33.2
15	CTE01A	*Catenula adhaerens*	21.1	10.9
16	GY014A	*Gyrosigma eximium*	20.8	6.9
17	NI083A	*Nitzschia constricta*	20.5	26.4
18	XXX399	*Denticula sundaysensis*	19.0	3.7
19	XXX565	*Achanthes delicatula* subsp. aff. *engelbrechtii*	19.0	4.0
20	XXX649	*Denticula subtilis*	18.5	10.7

The 2% maximum abundance limit was used as a cut of, with all species with a maximum abundance falling below 2% being excluded from all further analysis, unless otherwise indicated.

5.3.2 The diatom flora of individual Sites

At each Site a number of Samples were taken across the intertidal gradient and so the 25 Sites containing diatoms can be examined in terms of their individual diatom flora. Plots of species abundance (for all species with an abundance > 2%) at Sampling Points within all Sites can be seen in Appendix 3. Some of the more detailed plots are repeated in the text for illustrative purposes.

5.3.2.1 Alnmouth, North East

Alnmouth is a Site that appears to show a gradient from high marsh down to mudflats and sandy mudflats, see Figure 5.1. A small number of species occur exclusively on the saltmarsh Sites (AM1 and 2), such as *Gyrosigma eximium* and *Navicula dissipata,* whilst others occur at noticeably higher abundances on the saltmarsh Sites than further down the intertidal gradient, e.g. *Navicula gregaria, Navicula cincta* and *Navicula salinicola.* Taxa that are more abundant on the mudflat (AM6) and sandy mudfalt (AM7), such as *Achnanthes delicatula* subsp. *hauckiana* and *Catenula adhaerens* are also found in low abundances in the marsh Samples illustrating the taphonomic overprinting in the subfossil assemblages as described by Sherrod *et al.* (1989).

The creek Sample at Alnmouth (AM3), although taken from the creek cutting through the high saltmarsh, is actually a depositional environment close to that of the mudflat in terms of sediment properties and elevation, and hence inundation frequency. This is reflected in the similarity of the diatom flora between the creek and the mudflat, and the sandy mudflat. The diatom flora from Samples AM4 and AM5, both from the low saltmarsh, display a flora that is intermediate between the higher marsh Samples of AM1 and AM2 and the lower elevation tidal flats of AM6 and AM7. This reflects the fact that the low, or pioneer, saltmarsh is very much a transitional habitat between the open intertidal flats and the saltmarsh proper. AM4 and AM5 do show a number of floristic differences, however, most striking being that of the higher abundance of *Navicula salinicola* and *Navicula* sp. A in AM5. Whilst it is not possible to explain exactly what accounts for these differences, it should be pointed out that the higher

vegetation is different at the two Sites, AM4 representing the Annual *Salicornia* Saltmarsh Community (NVC community SM8) and AM5 representing the *Spartina anglica* Saltmarsh Community (NVC community SM6). *Spartina anglica* is known to affect some sediment properties such as degree and depth of anoxia (Frid et al., 1999) and it is therefore possible that the type of higher vegetation may affect diatom assemblages from pioneer marsh habitats. AM4 is also slightly sandier than AM5.

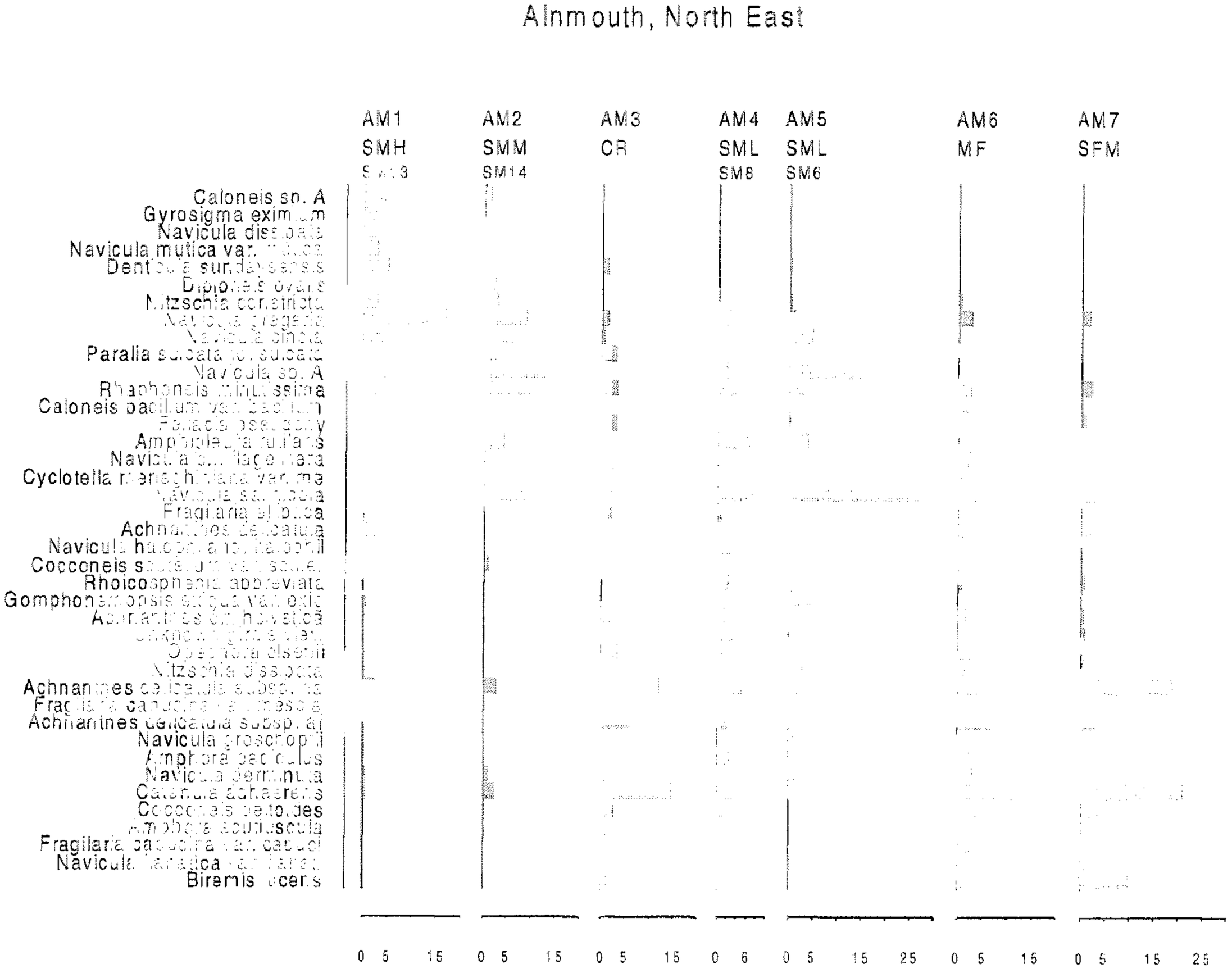


Figure 5.1 Diatom species distribution at Alnmouth

5.3.2.2 Aust, The Severn

Aust, in the mid Severn estuary has three Samples with diatom assemblage results. The mudflat and low saltmarsh Samples (AU5 and AU3 respectively) display very similar flora, with a dominance of *Rhaphoneis minutissima* and *Cymatosira belgica*. *Cymatosira belgica* is

also present in the middle marsh assemblage (AU6) but *Navicula cincta* replaces it as the most abundant species, dominating the Samples at over 50% abundance.

5.3.2.3 Blacktoft Sands, The Humber

This Site, from the confluence of the river Trent with the Humber estuary, is one of the furthest upstream Sites, in relative terms, in the dataset. Compared to other Sites, the diversity here is relatively low, with all Sites displaying an N_2 diversity value less than 10, apart from BK5 at an N_2 diversity of 13.9. The transect shows a distinct difference in the diatom flora between the mudflat Samples (BK1 and 2) a little above MHWN, and the Samples from the extensive *Phragmites australis* bed (BK4 and 5) extending from below to above MHWS. Dominant mudflat species here includes *Navicula phyllepta, Navicula flanatica, Navicula gregaria* and *Rhaphoneis minutissima. Rhaphoneis minutissima* is a constant species throughout the Site but the higher abundances in the mudflat Samples suggest the presence in the *Phragmites australis* Samples may be due to tidal deposition. If this is the case then the effects of tidal transportation appear to be selective as *Navicula phyllepta* and *Navicula flanatica,* both abundant on the mudflat, do not appear in significant abundances in the *Phragmites australis* beds. A further explanation could be that the distribution of *Rhaphoneis minutissima* is more closely related to sediment properties than it is to elevation but its frequent abundant occurrence on sandflats such as at Bowness-on-Solway favours the former hypothesis.

The diatom flora of the two *Phragmites australis* Samples are visibly different from each other with *Navicula cincta* dominating in the lower Sample (BK4) and a larger variety of taxa at lower abundance making up the bulk of the higher Sample (BK5), including *Nitzschia debilis*, *Denticula sundaysensis*, *Navicula mutica*, *Nitzschia clausii* and *Navicula cincta.* Possible reasons for the Sample from the high saltmarsh, *Scirpus maritimus* community, not containing diatoms are discussed in section 5.2.2.

5.3.2.4 Blackwater, Southern East Anglia

This southern East Anglia Site contains two mudflat assemblages with almost identical species composition although a little variety in terms of their relative abundance. Again, *Cymatosira belgica* and *Rhaphoneis minutissima* are present in high abundances in these tidal

flat Samples, but *Nitzschia fontifuga* and *Nitzschia sigma* are equally as important as these species at BW1, the lower of the two Sites.

5.3.2.5 Bowness-on-Solway, Solway Firth

Bowness-on-Solway is an interesting Site, having a high saltmarsh flat separated from the lower sandflats by a cliff. These two distinctive intertidal sections are reflected in a conspicuous difference in the diatom assemblages between the high marsh Samples (BS1 – 3) and the sandflat Samples (BS 5 – 6). The taxa that occur in both sections at an abundance of around 5% or more include the cosmopolitan *Navicula gregaria* and cosmopolitan and often abundant *Rhaphoneis minutissima*. The difference between these two dominant species at this Site being that *Navicula gregaria* is more abundant on the marsh whilst *Rhaphoneis minutissima* is more abundant on the sandflats. A clear pattern already seems to be emerging in relation to the habitat preference of *Rhaphoneis minutissima* and its ability to be transported up onto the saltmarsh. Some species' life-form and morphology do favour entrainment and transportation over others (De Jonge, 1985) and it would appear that *Rhaphoneis minutissima* might be one such species.

Sample BS2 comes from a wet pan between BS1 and BS3 progressing down the saltmarsh. The diatom flora in this sample bears a closer resemblance to the lower of the two high saltmarsh Samples (BS3) but is none the less distinctive in its own right. Most interesting is the predominance of *Navicula salinicola* and the significant abundance of *Plagiogramma van-heurckii* and *Plagiogramma pulchella* otherwise only found on the lower sandflats. Assuming the pan is frequently filled with water, if not through tidal inundation, then through precipitation, it is possible that these *Plagiogramma* species, as opposed to being allochthonous are actually autochthonous, favouring the wetter conditions, but this theory cannot be verified without further investigation of the saltmarsh pans.

5.3.2.6 Bridgewater Bay, The Severn

Once again, *Cymatosira belgica* and *Rhaphoneis minutissima* can be seen in Figure 5.2 to predominate across the whole transect, both species reaching maximum abundance on the mudflat. Interestingly, however, neither species feature on the sandflat Samples, which displays a flora that is quite distinct from the rest of the sampling points at the Site. Species unique to this sandflat Sample include *Navicula perminuta, Navicula praestoeensis, Navicula*

germanopolonica, Achnanthes lemmermannii, Navicula salinicola, Pseudostaurosira perminuta and *Biremis lucens.* Species with a much higher abundance within the sandflat Sample than at other sampling points include *Catenula adhaerens, Achnanthes delicatula subsp. hauckiana* and *Opephora marina var. minuta.* This all combines to give a very distinctive sandflat flora. This Sample, BB5, is made up of 71% medium sand, a relatively coarse sedimentary environment. Given the predominance of *Rhaphoneis minutissima* in more silty mudflat habitats at other Sites, this conspicuous absence from this one sandy Site at Bridgewater Bay may indicate a specific grain size preference for *Rhaphoneis minutissima* significantly finer than medium sand. The same may be said for *Cymatosira belgica.*

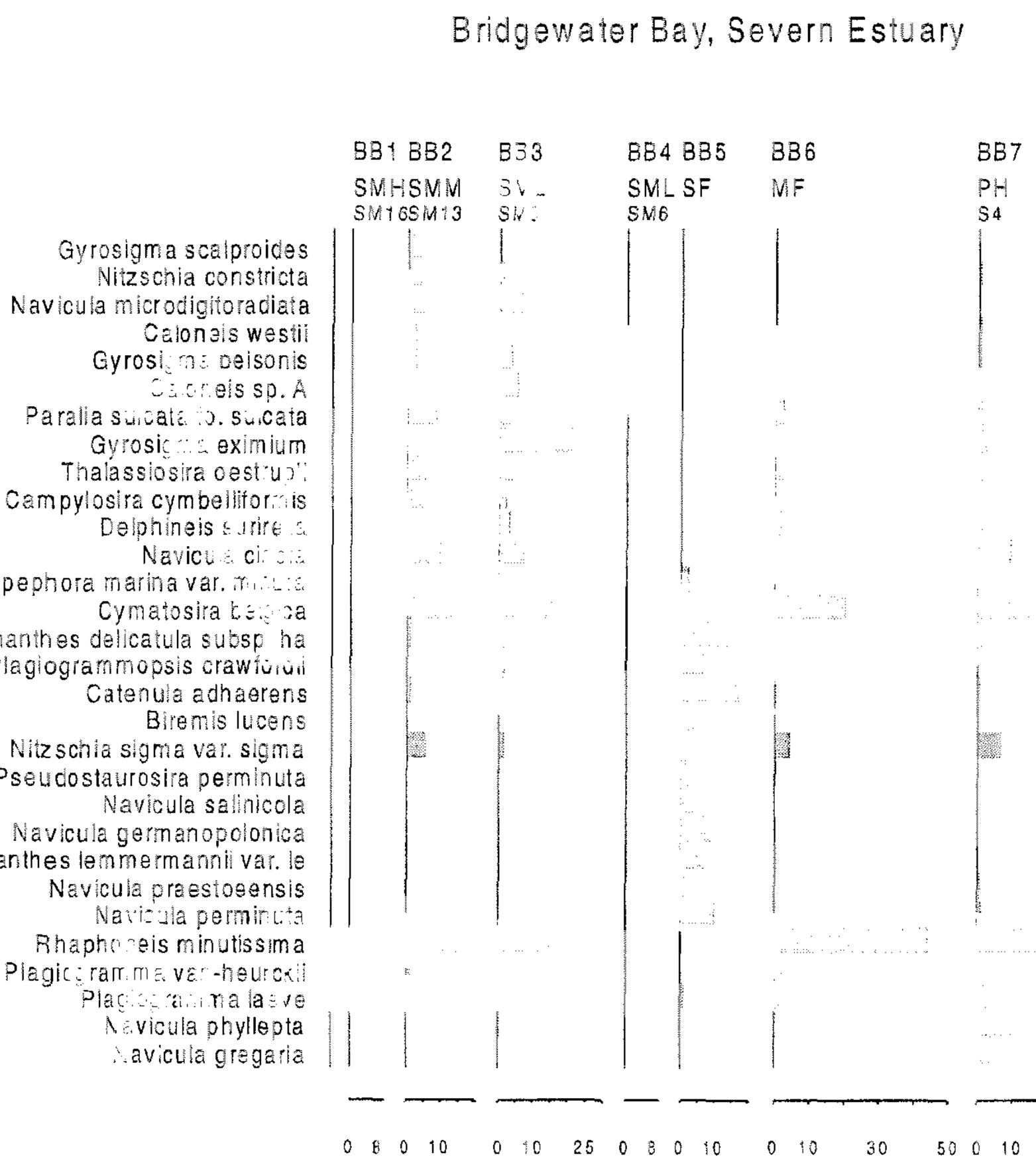


Figure 5.2 Diatom species distribution at Bridgewater Bay

Estuarine planktonic forms, i.e. *Paralia sulcata* and *Thalassiosira oestrupii*, feature in greater number and at higher abundances on the saltmarsh Samples (BB2 and BB3) than on the

intertidal flats (see Figure 5.2). This may reflect the reduction in energy of the flood tide as it reaches the saltmarsh causing the deposition of these planktonic forms that were held in suspension further down the tidal range. A distinctive autochthonous saltmarsh flora is also seen including some *Gyrosigma* spp., some *Caloneis* spp., *Navicula cincta* and *Navicula microdigitoradiata.*

Sample BB7, from the *Phragmites australis* bed at the back of the saltmarsh, shows affinities with both the saltmarsh and mudflat flora, most likely reflecting a combination of its altitudinal and surface sediment properties. Additional species, unique to this Sampling Site, include *Navicula phyllepta* and *Navicula gregaria*. These taxa frequently occur in other Sites above ML and *Navicula gregaria* appears to reflect the fresher environment. *Rhaphoneis minutissima* and *Cymatosira belgica* have a high relative abundance in the Phragmites sample. This may be due to a substrate preference predominating over an altitudinal preference, but, as suggested for the Blacktoft Sands *Phragmites* sample (section 5.3.2.3), it may also simply be due to tidal deposition in an environment with a low abundance of autochthonous diatoms.

5.3.2.7 Burnham, North Norfolk Coast

A number of sampling points at Burnham contain diatoms too badly preserved for analysis, as already discussed in section 5.2.2. There are therefore only two sampling Sites with diatom results, one being a dry pan on the high marsh surface (BH3) and the other a mudflat Sample (BH5). Considering the lack of identifiable diatom remains from other Sites, it is perhaps surprising that the dry pan did contain good diatom remains suggesting that the pan usually does contain water. The flora is very different between the two Samples with only three species in common at abundances much above 2%. These are the frequently occurring *Cymatosira belgica*, *Achnanthes delicatula* subsp. *hauckiana* and *Rhaphoneis minutissima*. All occur at higher abundances on the mudflat, again suggesting their appearance in the pan Sample may be allochthonous. The pan Sample does contain some species more usually associated with the higher saltmarsh, in which the pan in situated, including all taxa identified in section 4.5.1.1 as coming from the *Navicula microdigitoradiata* complex.

5.2.3.8 Caerlaverock, Solway Firth

The diversity of species across the transect at Caerlaverock in the inner Solway Firth is high, although N_2 diversity at individual Sampling Sites does not exceed 15. Three species dominate the transect; these are *Rhaphoneis minutissima*, *Navicula salinicola* and *Navicula gregaria*, seen clearly in Figure 5.3. *Navicula salinicola* occurs at a relatively consistent high abundance between 10 and 15% across the transect, apart from the pack saltmarsh Sample (CK6) where it only reaches an abundance of 3%. The back of the saltmarsh is a much fresher environment marking the very upper limit of tidal inundation and the transition to a terrestrial habitat. *Navicula salinicola* is clearly only present as an allochthonous addition to the flora here, which is dominated by *Navicula gregaria* with a number of other fresh and oligohaline taxa including *Fragilaria famelica*, two *Pinnularia* spp., *Navicula mutica* and *Achnanthes lanceolata*. *Navicula gregaria* displays a marked increase in abundance up the tidal range, peaking in this back saltmarsh Sample.

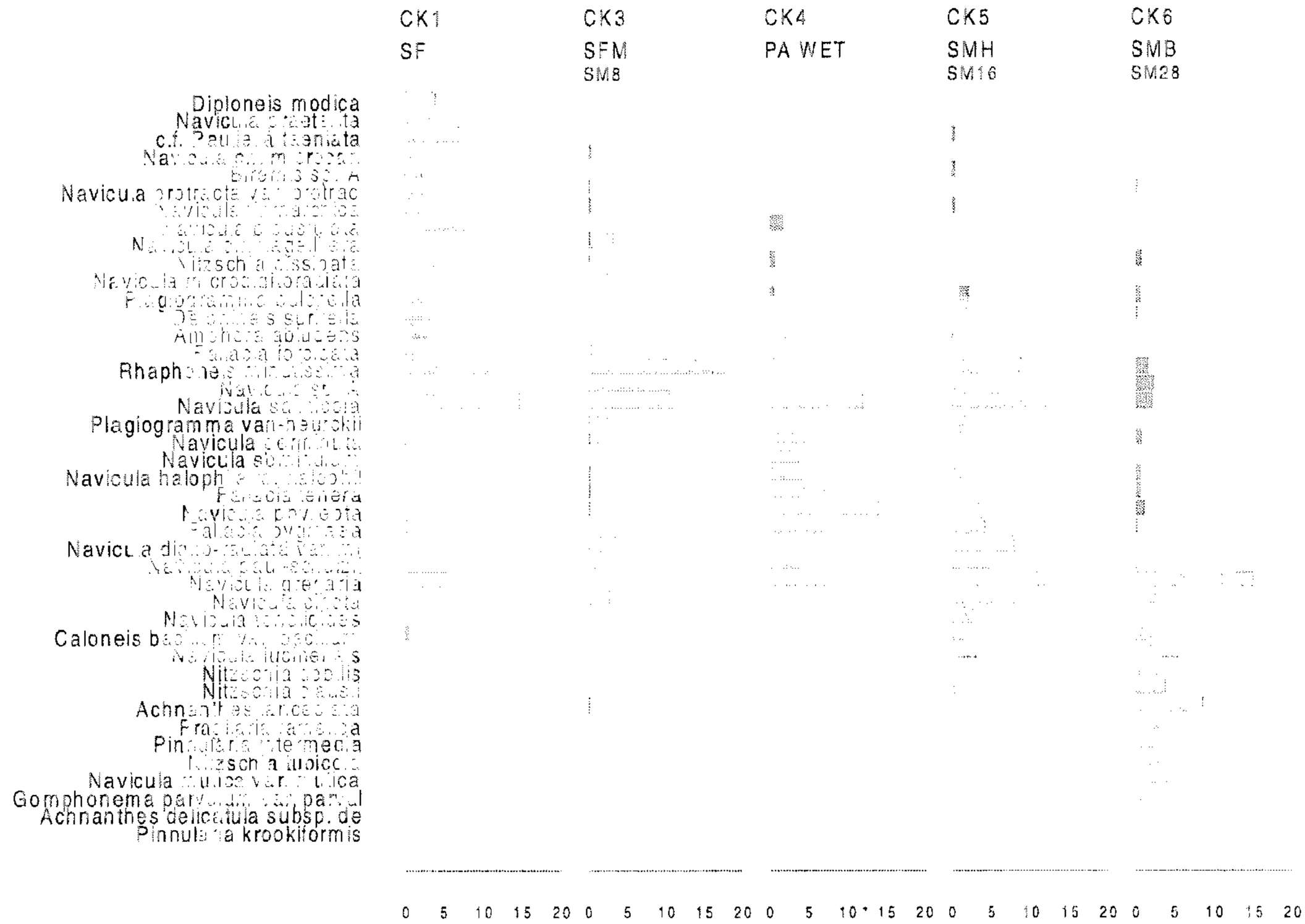


Figure 5.3 Diatom species distribution at Caerlaverock

If *Navicula salinicola* and *Rhaphoneis minutissima* are ignored for a moment then the distinctive different between the sandflat Sample (CK1) and saltmarsh Samples (CK4 to 6) becomes apparent and a clearer gradient across the transect can be seen. The sandflat Sample has a number of unique taxa identifying it as a very different intertidal habitat, and these can be seen at the top left of the plot in Figure 5.3. The slightly higher elevation muddy sandflat (CK3) is harder to characterise, sharing species equally with the sandflat, wet pan and high saltmarsh Samples. One distinctive feature, however, is the domination of the Sample by three species, *Rhaphoneis minutissima*, *Navicula* sp. A and *Navicula salinicola*. *Navicula* sp. A appears at 11% abundance and elsewhere never exceeds 2%.

The wet pan Sample (CK4) is also interesting showing affinities with the sandflat, muddy sandflat and high saltmarsh. The closest similarities are with the high saltmarsh within which the pan is situated. The pan is quite a deep primary pan, over 6 inches deep, and it is therefore likely that it very rarely dries out, acting more like a small pond.

5.3.2.9 Deben, Southern East Anglia

The four Samples from this Site do not display any perceptible gradient. Species predominating across the whole transect include *Navicula halophila*, *Nitzschia constricta*, *Nitzschia fontifuga*, *Navicula phyllepta*, *Cymatosira belgica* and *Rhaphoneis minutissima*. The sediment properties of these Samples are all very similar with silt making up between 67 and 78% of the sediment. Also the presence of a sea wall along the Deben restricts the development of the intertidal transition above the pioneer saltmarsh zone, so the difference in the habitats in terms of elevation is also small. The only main difference between Sites is the higher vegetation in the two low saltmarsh Samples, one from an Annual *Salicornia* Saltmarsh Community (DB1) and the other from a *Spartina anglica* saltmarsh community (DB3). Whilst having almost identical species listed, these two Samples do appear to have some differences in terms of the abundance of taxa.

5.3.2.10 Exe, South Coast

The Exe is similar to the Deben in the artificial restriction of the development of the intertidal transitional to saltmarsh communities. Mudflat is the only habitat present, although sediment properties do change, becoming muddier as the elevation drops from the sea wall. This

elevation drop towards the main channel is reflected in a clear zonation of macroalgae in the lower section of the flats. The flora of the two Samples analysed are very similar with both being dominated by *Achnanthes delicatula* subsp. *hauckiana* and *Catenula adhaerens* with large proportion of the lower abundance taxa in common. There are, however, differences in abundances between sites, as well as some species individual to each. EX1 is the higher and sandier of the two Samples reflected in the presence of *Navicula germanopolonica* and lower abundances of some epipelic species such as *Navicula phyllepta* and some *Nitzschia* species. The properties of the sediment appear to be the main environmental variable driving the differences between two otherwise very similar assemblages.

5.3.2.11 Frampton, The Wash

An interesting point of note at this Site is the differences between the diatom flora of the two low saltmarsh Sites (FR3 and FR5). There are, however, very important differences in the environmental properties of the two Sites, which the NVC communities reveal; FR3 being an open *Spartina anglica* Saltmarsh Community and FR4 being a *Halimione portulacoides* saltmarsh community. *Halimione portulacoides* can extend down into the low saltmarsh where conditions are right (Rodwell, 2000). This particular Site, FR4, was at the top of a creek bank, still at low elevation and before the saltmarsh vegetation had changed significantly to a mid marsh community. The dense *Halimione portulacoides* would provide much greater shade compared to the open *Spartina anglica* and is also situated at a point with good drainage leading to a much lower water content than the *Spartina anglica* marsh. Although both are predominantly silty substrates, FR4, the *Halimione portulacoides* habitat has a higher proportion of sand and lower proportion of silt compared to FR3. These differences, despite the similarity in elevation, must account for the differences in diatom flora, and in particular the high abundance of *Navicula cincta* at FR4, showing greater similarities to the equally shady and well drained high marsh Sample, FR6.

Apart from this discrepancy discussed above, and the ubiquitous *Rhaphoneis minutissima*, there is again a strong gradient in the diatom flora across the transect.

5.3.2.12 Gibraltar Point, The Wash

This site is characterised by a narrow section of high saltmarsh leading to a large, deep creek. The Sample taken from the muddy rolling bank of this large creek (GP4) has been categorised

as a mudflat as the habitat here is more similar to a mudflat than to the bottom of a creek. The diatom flora from this Sample is certainly distinct from the other Samples, having a higher abundance of *Rhaphoneis minutissima* and *Plagiogramma laeve* (both found at an abundance of 5% or more throughout the transect), a very low abundance of species found to be more prevalent on the high marsh and its creek (GP2), plus a number of unique taxa including *Navicula nolens*, *Amphora tenuissima* and c.f. *Pauliella taeniata*.

The other three Samples, from within the high saltmarsh environment over the bank of the large creek, are also interesting. The creek Sample, GP2, and the high saltmarsh Sample GP3 display a very similar flora with the main differences being in species relative abundance. Despite the difference in elevation of these two Samples this similarity in diatom flora is perhaps not too surprising given that that GP3 is taken from the top of the bank of the creek in which GP2 in taken. GP1 is also a high saltmarsh Sample but has a flora distinctly different from that found at GP2 and 3. GP1 is in fact at a higher elevation, above MHWS and a very different habitat in terms of vegetation, being a closely vegetated *Puccinellia maritima* Saltmarsh Community, compared to the freely draining *Halimione portulacoides* Saltmarsh Community of GP3.

Navicula cincta and *Navicula digitoradiata* var. *minima*, in keeping with many other transects in this study, appear in significant abundance on all three Sites within the high marsh but are absent from the mudflat Sample. *Navicula phyllepta* and *Navicula salinicola* have a far higher abundance within the high saltmarsh than they do on the mudflat.

5.3.2.13 Hamford Water, Southern East Anglia

As with a number of other transects, *Cymatosira belgica* and *Rhaphoneis minutissima* maintain a high abundance throughout the transect never falling below 5% abundance, but peak on the mudflats (HW 5 and 6) and sandy mudflat (HW1) in Figure 5.4. *Navicula ramosissima* and *Nitzschia fontifuga* also maintain a constant presence, again tailing off in the mid (HW4) and back saltmarsh (HW7). The Samples seem to fall into three groups in terms of the diatom flora; both mudflat Samples are very similar, as are the sandy mudflat and low saltmarsh (the later developing from the former) and the mid saltmarsh and back saltmarsh form the third group. No true high saltmarsh habitat develops at this Site due to the presence of a flood embankment, although the back saltmarsh is more waterlogged and peaty, with a very different vegetation community to the rest of the marsh. The back saltmarsh does

display some discrete differences from the mid saltmarsh in the high abundance of *Cocconeis scutellum* and *Denticula subtilis*. Witkowski (2000) comment that *Denticula subtilis* was sometime found in abundance at wastewater outflows. At this particular back saltmarsh there were a number of signs of pollution in terms of eutrophication, such as thick algal growth in standing water. It is therefore possible that the high abundance of *Denticula subtilis* at this Site is, in part, a result of the artificially elevated nutrient content.

Hamford Water, South East Anglia

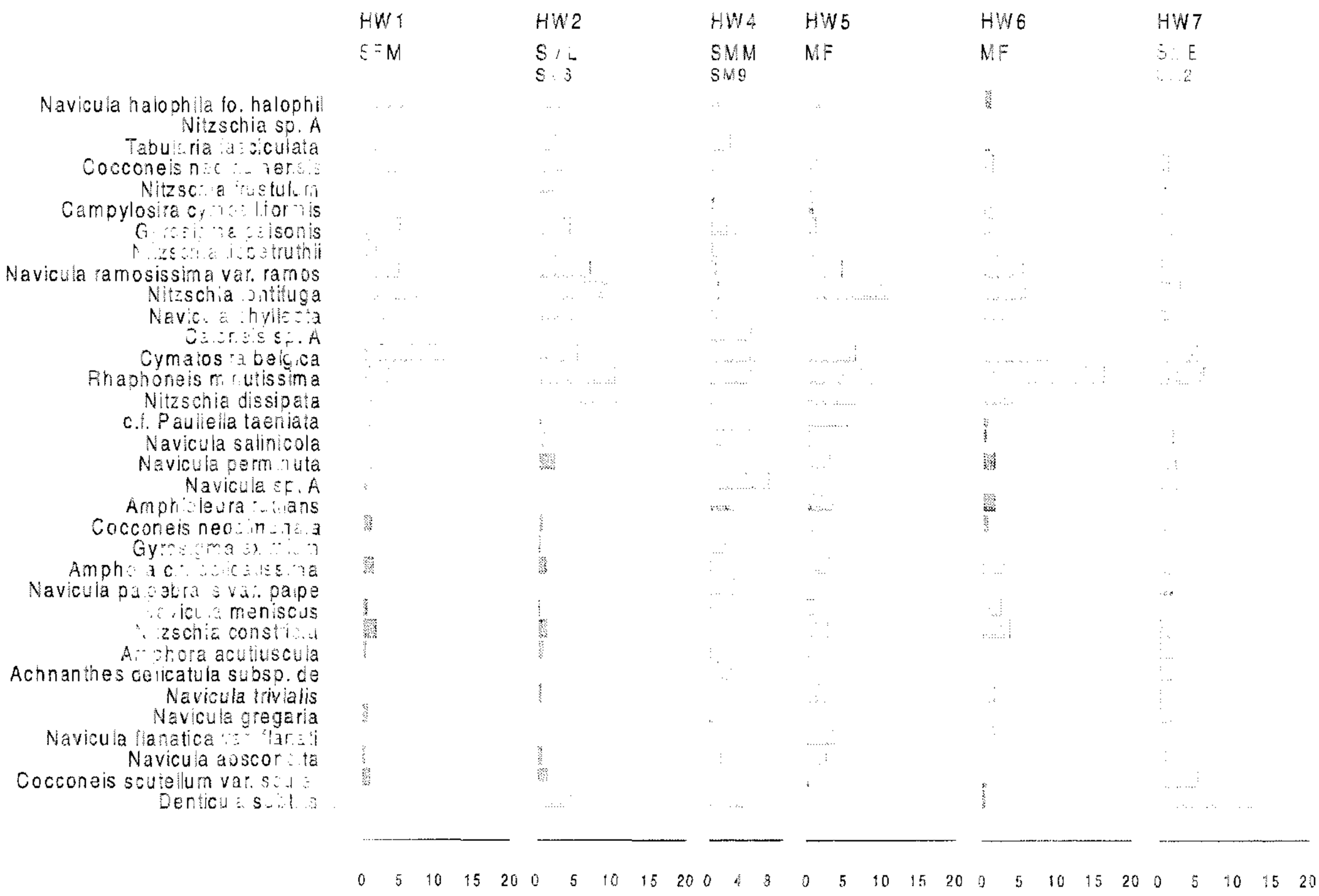


Figure 5.4 Diatom species distribution at Hamford Water

The mid saltmarsh (HW4) has a markedly higher N_2 diversity values than the other Sites at 26.3 with the others ranging from 14.5 – 18.5. Like other low and mid saltmarsh Sites this may reflect the transitional nature of this habitat and the proximity of very different diatom floras on back saltmarsh and lower intertidal flats.

In contrast to some other Sites such as Gibraltar Point, where *Navicula halophila* is found at high abundance on the high saltmarsh (a community absent from this Site), *Navicula halophila* is most abundant on the low saltmarsh and sandy mudflat.

5.3.2.14 Holy Island, North East

At this Site there does appear to be a gradient in the diatom flora across this transect leading down to a particularly unique sandflat flora at HI7. Apart from *Navicula* sp. A and *Navicula salinicola*, which are present at of above 5% abundance at each sampling point, HI7 contains a group of characteristically sandflat taxa such as *Navicula germanopolonica* and *Navicula perminuta*. A small *Achnanthes delicatula* species (discussed in section 4.5.1.1) is also present at abundance greater than 5% but does not occur in any other Samples, whilst *Achnanthes delicatula* subsp. *delicatula* occurs throughout the Site, peaking in the mid saltmarsh Sample HI3. This difference in distribution strengthens the case for recording the small *delicatula*-like species as a separate species, although there is the possibility that the small species found on the sandflats is simply an ecotype of *Achnanthes delicatula* subsp. *delicatula*, restricted in size due to the harsh nature of the sandflats environment. Further investigation of this apparently distinct species would be needed to confirm this hypothesis.

The flora of the low saltmarsh (HI5) appears to show a transition from the sandflats up to the mid saltmarsh with *Navicula microdigitoradiata* markedly dominant at 27% abundance. Taxa that appear to be characteristic of the mid saltmarsh at Holy Island include *Caloneis westii*, *Caloneis* sp. A, *Navicula digitoradiata var minima* and *Navicula cincta;* a pattern observed at a number of other Sites.

The three mid saltmarsh Sites do show a variation in flora, which is not surprising as the Samples rise in elevation from HI3 to HI1. HI1 is almost a high saltmarsh community but a little too far below MHWS to categorise it as such and with vegetation very similar to the other two mid saltmarsh Samples.

5.3.2.14 Lymington, South Coast

This is an interesting Site as it does not consist of a gradual transition through intertidal habitats but instead comprises a large block of high saltmarsh habitat intersected by creeks (one of which effectively cuts the saltmarsh off from the land) and separated from the low mud and sand flats by a sharp cliff some 100 cm high. Hence, the only Samples at the Site come from the high saltmarsh environment and the mudflat, rather like Bowness-on-Solway. Given the nature of the Site it is not surprising that the mudflat Sample, whilst having some species in common with the Sample taken from the creek that bisects the high saltmarsh

(LY5), has a flora very different to the high marsh Samples LY1, 3 and 4, with *Cocconeis scutellum* and *Tabularia tabulata* dominating the assemblage. Nonetheless there are some species that are present consistently throughout the Site, the most prominent being *Cocconeis scutellum* and *Rhaphoneis minutissima*, but also *Nitzschia fontifuga*, *Navicula perminuta*, *Paralia sulcata*, *Nitzschia constricta*, and *Cymatosira belgica*. LY5, the Sample from the creek that bisects the high saltmarsh block, has a similar flora to the mudflat but also contains, at a low abundance, a number of species more common in the high saltmarsh Samples.

The other three Samples from the high saltmarsh (LY1, 3 and 4) display a broadly similar flora with *Navicula salinicola*, *Denticula subtilis*, *Navicula* sp. A, *Navicula microdigitoradiata* and *Rhaphoneis minutissima* ranking amongst the most abundant. The Sample from a creek up in the high saltmarsh (LY1) is very similar floristically to the high saltmarsh Samples LY3 and 4, with the addition of some uniquely abundant taxa including *Navicula halophila*, *Stauronies salina*, *Navicula phyllepta* and *Fallacia pygmea*.

5.3.2.15 Mawddach, Wales

The two distinct zones in the intertidal environment of the Mawddach estuary mouth are reflected in two distinct diatom floras; one from the broad rolling sandbanks and sandy creeks out in the middle of the estuary (MD1, MD2 and MD3), and one from the saltmarsh (MD6 and MD7). Species characteristic of the sandy habitat here include *Achnanthes delicatula* subsp. *hauckiana*, *Navicula germanopolonica*, *Navicula perminuta*, *Opephora olsenii*, *Fallacia cassubiae* and *Fallacia tenera*. *Navicula gregaria* is the most abundant species in each of the sandy Samples and occurs in both saltmarsh Samples but at much lower abundance. This is in stark contrast to Sites such as, Alnmouth, Bridgewater Bay, Caerlaverock and Wigtown where *Navicula gregaria* has increased in abundance in the higher elevation Samples. *Rhaphoneis minutissima* is once again constant throughout the Site peaking in one of the sandflat Samples (MD2).

The low saltmarsh (MD6) and high saltmarsh (MD7) have a similar floristic composition in terms of species but are clearly two distinct groups in terms of relative abundance and a number of unique keys species, e.g. in MD7 the most abundant species is *Achnanthes delicatula* aff. *engelbrechtii* but this species does not occur in the low marsh Samples, possibly due to differing sediment characteristics.

5.3.2.16 Poole Harbour, South Coast

On first inspection Poole Harbour does not appear to show any specific trend in terms of the diatom flora, with *Navicula gregaria* and *Navicula phyllepta* dominating all four Samples from the mudflats up through the *Phragmites australis* bed. This is a microtidal site and would therefore be unlikely to show the type of distinct vertical zonation found in many macrotidal sites, hence the more homogenous flora across the transect at Poole Harbour. Nevertheless, whilst there are a number of other lower abundance species common to all four Samples, the two mudflat Samples (PH3 and 4) and the two *Phragmites australis* Samples (PH1 and 2) then appear to each have a set of diatoms characteristic of the two different environments. PH1, the higher elevation *Phragmites australis* Samples, and PH4, the lower elevation mudflat Sample, show the strongest contrast. Species associated uniquely with the *Phragmites australis* beds include *Navicula perlepida*, *Achnanthes delicatula* subsp. *delicatula*, *Navicula mutica* and *Amphipleura rutilans*, whilst species associated more strongly with the mudflats include a number of *Amphora* species, *Navicula praestoeensis* and *Navicula paul-schulzii*.

5.3.2.17 Sailor's Holme, The Wash

The diatom flora from the 8 Sailor's Holme Samples, stretching from the high saltmarsh to the intertidal flats display a distinct gradient in Figure 5.5, although this becomes a little blurred in the middle Samples around the low saltmarsh. *Rhaphoneis minutissima* and *Navicula salinicola* are present consistently throughout the transect whilst *Navicula microdigitoradiata* and *Navicula cincta* occur in all but the muddy sandflat Sample (SFM). *Navicula cincta* is particularly dominant in the high saltmarsh Sample (SH1), accounting for almost 40% of the count. It then reduces rapidly in abundance across the Site as the elevation drops.

Two low saltmarsh Samples, SH4 and 5 have highly comparable diatom assemblages despite marked differences in higher vegetation. However, the third low marsh Sample, SH7, shares a number of species in common with the creek and muddy sandflat Samples, albeit in lower abundance. This can be explained by SH7 occurring beyond the creek Sample, at the very lowest edge of the pioneer marsh community, with only a sparse covering of *Salicorina* spp. and therefore being closer in character to the open tidal flats than to the other low saltmarsh habitats. Species common and relatively abundant in the creek and sandy mudflat Samples

include *Navicula perminuta*, *Fragilaria atomus*, *Fragilaria cassubica* and *Navicula praestoeensis*. These species all occur at low abundances in the three low saltmarsh Samples, but do not feature on the mid and high saltmarsh and thus clearly represent a low elevation community.

The wet pan Sample (SH3) appears to be a mixture of the low and mid saltmarsh floras, as might be expected given that the Sample comes from within the mid saltmarsh, but its water content and elevation are closer to the low saltmarsh.

Unlike some other Sites there is no apparent pattern to the distribution of *Rhaphoneis minutissima* at Sailor's Holme, suggesting a large degree of taphonomic overprinting, although it is conspicuous in its absence from the sandy mudflat Sample, SH8.

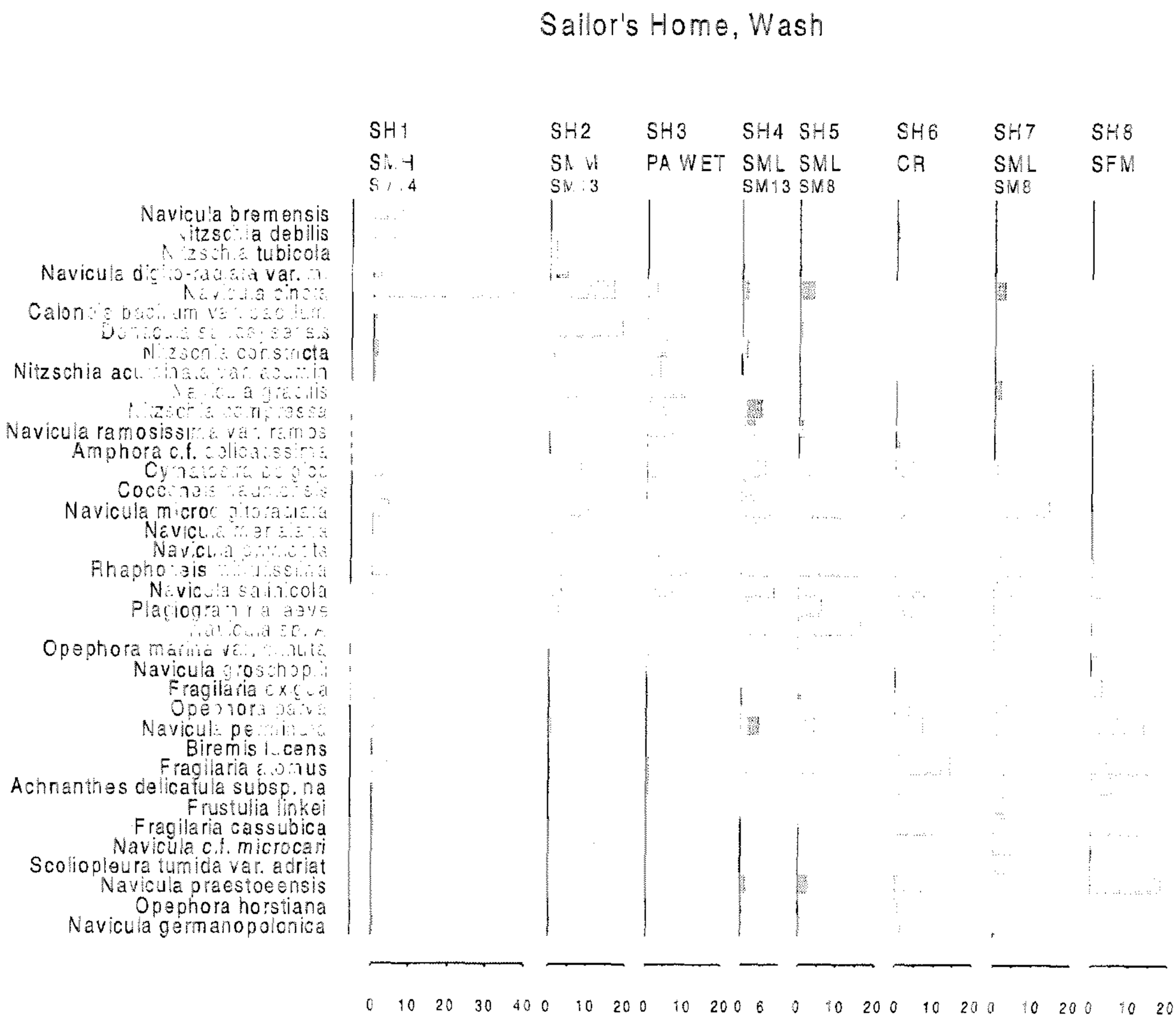


Figure 5.5 Diatom species distribution at Sailor's Holme

5.3.2.18 Skyreburn Bay, Solway Firth

SB4, the higher sandflat Sample has a low N_2 diversity of 6.5 especially when compared to the lower sandflat Sample SB5 with an N_2 diversity of 22. This low diversity at SB4 accounts for the high abundances of those species that are found. There is not a particularly strong diatom floristic gradient at this Site, with a large number of species occurring throughout at various abundances, possibly due to tidal mixing. Nonetheless there are a small number of species that separate the higher mudflat assemblage (SB1) from the lower sandflat Sample (SB5) with *Navicula paul-schulzii*, *Odentella aurita*, *Nitzschia capitellata*, *Achnanthes minutissima* and *Amphora copulata* distinguishing the mudflat and c.f. *Pauliella taeniata*, *Navicula nolens*, *Navicula* sp. A, *Stauroneis salina*, *Nitzschia dissipata* and *Nitzschia palea* distinguishing the sandflat.

5.3.2.19 Spurn Marsh, Humber

Rhaphoneis minutissima again appears at high abundance throughout the transect, with no clear pattern to its distribution. The lower mudflat Sample (SM5) assemblage, as well as containing a high abundance of *Rhaphoneis minutissima*, is characterised by a distinctive assemblage comprising *Navicula gracilis, Nitzschia debilis, Navicula digitoradiata* var *minima, Gyrosigma eximum* and *Gyrosigma peisonis* and *Nitzschia capitellata, Nitzschia sigma* and *Nitzschia fontifuga*. This is a particularly interesting assemblage as a number of the abundant species have otherwise been found to be indicative of saltmarsh habitats; in particular the *Gyrosigma* species, *Navicula digitoradiata* var *minima* and, especially, *Navicula cincta*. *Navicula cincta* displays a large degree of morphological variation in terms of size, central area shape and striae density (discussed in Archibald, 1983 and Carter, 1979). It is possible that the *Navicula cincta* species dominating the mudflat assemblage is a morphological variation within the *cincta* complex that has different ecological preferences, but the presence of other saltmarsh species suggests that this could indeed be *Navicula cincta* proper and that this habitat has some specific qualities that favour this taxon. Part of the explanation may lie in the particular morphology of the mudflat at this Site. The mudflat is made up of parallel ridges and creeks with approximately 2 to 4 cm difference in height, as described in the Site description for this Site (section 3.3.3.3). The Sample in question is taken from the centre of one of the ridges. Not only is it, therefore, at a slightly higher elevation than the average surface of the mudflat and hence has a shorter inundation period, but it is also drier than most mudflats with the surface water draining away into the slightly

lower creeks. The ridges may therefore favour more aerophilous diatoms than the surrounding lower mudflat creeks.

Moving up the intertidal environment the creek and ridge system increases in height difference and SM3, recorded as being a wet pan is in fact taken from the base of one of the parallel creeks that occasionally broadens out into a round pan near the edge of the inception of the pioneer marsh. This Sample shows close similarities to the low marsh assemblage (SM2), both being dominated by *Navicula perminuta*, *Biremis lucens*, *Achanthes delicatula* subsp. *hauckiana*, *Achnanthes lemmermannii* and *Rhaphoneis minutissima* with both habitats containing just a small number of unique taxa. The mid saltmarsh Sample (SM1) is again similar to the low marsh Sample being dominated by the same species listed above but at higher relative abundances, and with a number of other taxa also distinguishing this habitat including *Navicula meniscus* and *Fragilaria pinnata*.

5.3.2.20 Spurn Point, Humber

This transect consists of three intertidal sandflat Samples with SP1 at the highest elevation and SP3 at the lowest. In general terms the three diatom assemblages are highly similar. The key difference is the dominance of *Navicula arenaria* in SP3 effectively reducing the abundance of the other species present, nearly all of which are all found in the other two Samples. The predominance of *Navicula arenaria* in this Sample is discussed in section 5.3.1. Leaving *Navicula arenaria* aside, the flora at these three Sites is highly characteristic of sandflats with open marine conditions and the specie that, together, indicate this include *Navicula perminuta, Amphora wiseii, Cocconeis neothumensis, Cocconeis hoffmanii* and *Cocconeis distans*, *Fallacia cassubiae, Navicula salinicola* and *Navicula germanopolonica*. A number of these, such as *Navicula germanopolonica, Navicula perminuta* and *Fallacia cassubiae* are identified as sandflat diatoms from other Sites described, above.

5.3.2.21 Stiffkey, North Norfolk Coast

As with many Sites, a small number of taxa obscure the otherwise more distinct gradient in the diatom flora across the Site, shown in Figure 5.6; these species include the ubiquitous *Rhaphoneis minutissima* with *Cymatosira belgica* occurring in tandem at a lower abundance, and *Navicula salinicola*. A sandflat flora emerges from Samples SK1 and SK8, characterised by *Amphora pediculus*, *Navicula perminuta*, *Fallacia cryptolyra, Navicula microcephala* and

Navicula germanopolonica. A number of additional indicative sandflat species occur in the lowest sandflat Sample, SK8, including *Fallacia cassubiae, Achnanthes delicatula* (small) and *Fragilaria cassubiae*, thus increasing the diversity of SK8 from the very low diversity of SK1 (N_2 diversity 18.7 and 4.3 respectively).

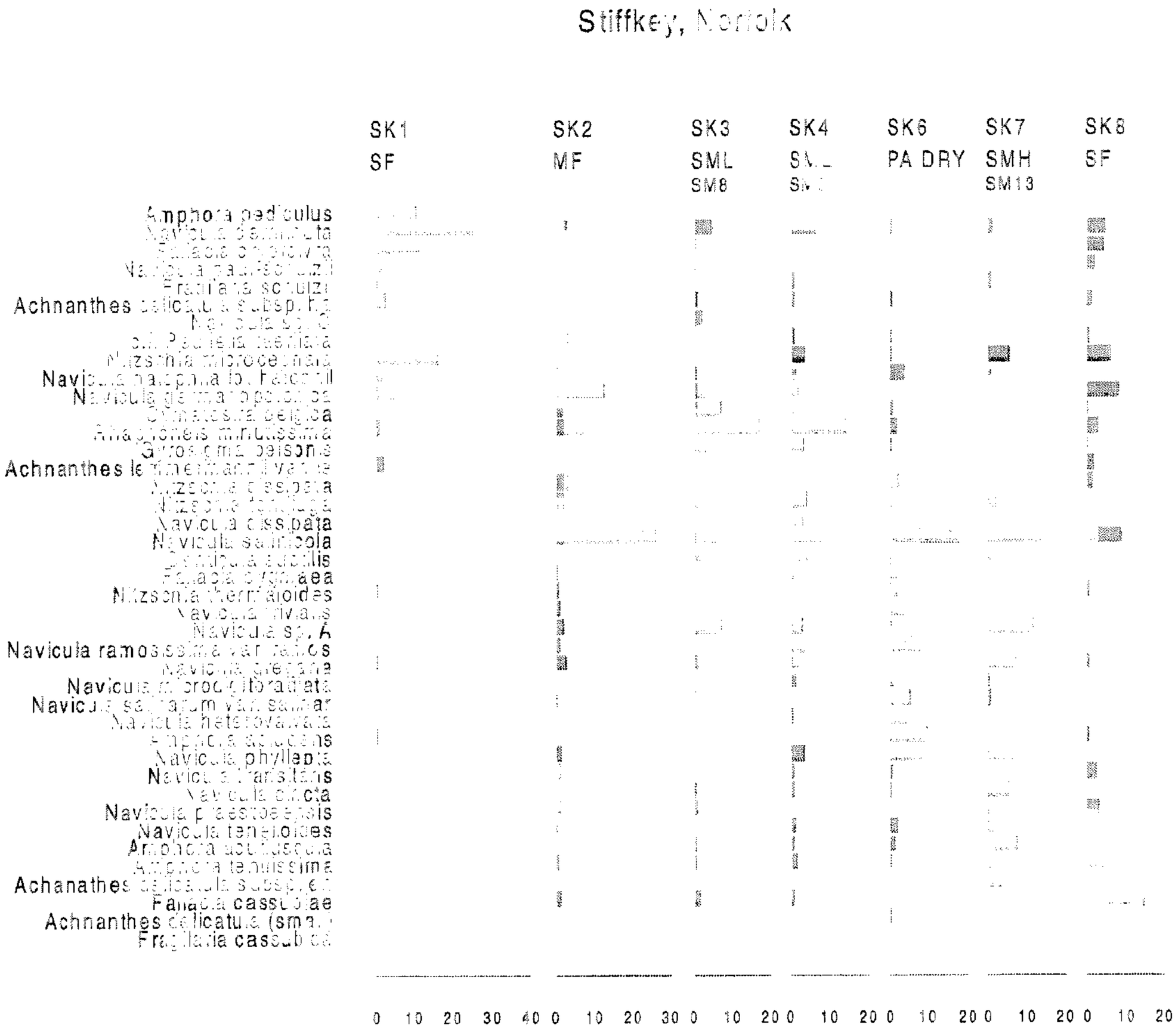


Figure 5.6 Diatom species distributions at Stiffkey

The mudflat and two low saltmarsh Samples (SK2, 3 and 4) have broadly comparable assemblages, with one of the main differences being the significantly higher abundance of *Navicula salinicola* in the mudflat Sample (SK2), although the lower diversity of this Sample compared to the low saltmarsh Samples may account for the higher relative abundance of this species in this Sample. The dry pan (SK6), from within the high saltmarsh and high saltmarsh (SK7) Samples have a number of species in common with the lower saltmarsh communities, but each has a group of uniquely abundant taxa distinguishing them from the other saltmarsh habitats. The pan is distinguished by its abundance of *Navicula ramosissima, Navicula*

salinarum, Navicula heterovalvata and *Navicula phyllepta* and the high saltmarsh by its abundance of *Navicula phyllepta, Navicula cincta,* and *Navicula tenelloides*, and *Amphora acutiuscula* and *Amphora tenuissima*. These two Samples from within the high saltmarsh habitat contain very little of any of the species listed above as being indicative of the sandflat at Stiffkey.

5.3.2.22 Welwick

A gradient can be seen in the diatom assemblages from mudflat through to high saltmarsh with a very high abundance of *Rhaphoneis minutissima* across all samples in the Site, as a consequence making it the only species obscuring the elevation/habitat gradient. Horton (1997) also found *Rhaphoneis minutissima* to be a dominant species from Welwick Marsh. Both the lower mudflat Samples (WK1 and 2) and the wet pan Sample (WK3) from a shallow pan on the mudflat surface, have analogous floras with *Biremis lucens, Achnanthes delicatula* subsp. *hauckiana*, *Achnanthes lemmermanii, Navicula perminuta* and *Rhaphoneis minutissima* forming the most important species in varying abundances. The higher mudflat Sample, WK4, coming just before the inception of the pioneer marsh, has a rather different and less diverse assemblage dominated mainly by *Rhaphoneis minutissima* and *Stauroneis salina*. Moving up into the pioneer marsh, from which the low saltmarsh Sample WK5 is taken, the assemblage looks very similar to wet pan assemblage of WK3, but overall is more closely related in terms of species and their abundances to the mid saltmarsh Sample WK6. The mid and high saltmarsh Samples (WK6 and 7 respectively) are alike, both containing a significant abundance of *Gyrosigma peisonis, Navicula cincta, Navicula gregaria, Navicula* sp. A, and *Nitzschia fontifuga* with a number of unique species occurring on the high saltmarsh, namely *Nitzschia debilis, Nitzschia lorenziana, Nitzschia microcephala* and *Navicula bremensis*.

5.3.2.23 Wentloodge, The Severn

The Wentloodge Site, towards the mouth of the Severn estuary, also displays a dominance of *Rhaphoneis minutissima* in tandem with a slightly lower abundance of *Cymatosira belgica* across the whole transect. The two high saltmarsh Samples, WL5 and WL6 share a number of common taxa including taxa commonly found on high saltmarshes in this study, such as *Navicula phyllepta, gregaria* and *digitoradiata* var *minima*. The higher Site, WL6 has a slightly higher diversity including the taxa *Navicula salinicola, Navicula flanatica* and

Navicula microdigitoradiata, Nitzschia constricta, Amphora c.f. *delicatissmia* and *Amphora coffeaeformis*. All the aforementioned species, with the obvious exception of *Rhaphoneis minutissima* and *Cymatosira belgica* hardly feature in any of the mudflat Samples, of which there are four across a distinct drop in elevation. Species common to most, if not all, of the mudflat Samples include *Navicula praeterita, Delphineis surirella*, and *Plagiogramma vanhaeurkii*.

Three estuarine planktonic species *Paralia sulcata* and two *Thalassiosira* occur in low to medium abundances across the Site and may obscure elevation and habitat relationships.

5.3.2.24 Wigtown, Solway Firth

The distinct intertidal habitat zonation at this Site is reflected in the diatom flora with all Samples not only sharing a number of common taxa with proximate Sites, but also exhibiting their own unique species, are displaying a gentle gradient in the diatom flora from the muddy sandflat (WT1) through the low saltmarsh (WT3) and high saltmarsh (WT5) to the back saltmarsh (WT6). Four species in particular reflect this gradient. *Rhaphoneis minutissima* and *Navicula salinicola* whilst present throughout the Site, reduces in abundance up the tidal gradient, the former more distinctly. Conversely, *Navicula gregaria* and *Navicula cincta* increase in abundance up the tidal gradient.

The back saltmarsh Sample (WT6) has a very low N_2 species diversity of 3.8 (all other Samples being greater than 10) suggesting that either few species can tolerate the conditions of this habitat or that preservation is poor. Further inland along the Solway Firth the back saltmarsh Sample at Caerlaverock is also dominated by *Navicula gregaria,* but has a significantly higher N_2 diversity at 12.4. The Wigtown back marsh Site may therefore experience more fluctuating conditions in terms of water content and salinity which would not only enable fewer species to adapt to the conditions but also reduce specie preservation due to repeated drought. A surprising feature of WT6 is the presence of *Navicula germanopolonica* at around 5% abundance. This species has only tended to appear as a significant proportion of the assemblage in sandflat Samples in other Sites. Whilst it would be straightforward to assume that its presence is autochthonous, it is surprising that it is not found in the muddy sandflat and low saltmarsh Samples, even at a low abundance, brought in from the inaccessible sandflats further out into the bay. This may be due to preferential deposition due

to reducing tidal energy across the saltmarsh, as suggested for *Paralia sulcata* deposition on the high saltmarsh at Bridgewater Bay (section 5.3.2.6).

5.3.2.25 Discussion of the distribution of diatoms at individual Sites

A number of features stand out from the description of the changes in the diatom assemblages across the tidal gradient at each Site. The most striking is the frequent dominance of *Rhaphoneis minutissima*, often accompanied by *Cymatosira belgica*. *Rahphoneis minutissma* was first identified by Hustedt in 1939 and classified as euryhaline (Hustedt, 1927-1966). This classification as a species that can tolerate wide variations in salinity is in keeping with its diverse distribution across the study area. Given the apparent widespread distribution of this taxon it is very surprising that it features in few floras addressing coastal and marine diatoms. It is tentatively identified by Hartley (1996) but does not feature in any of the other floras listed in section 4.5.1. It is possible that this species has been misidentified in the past as a small form of *Delphineis surirella*, (a species originally placed in the *Rhaphoneis* genus, (see Round *et al.*, 1990)) as the larger specimens do begin to resemble this species, but some subtle yet specific morphological features clearly separate the two species. The most distinctive morphological feature, usually resolvable in light microscopy, distinguishing species of the *Rhaphoneis* genus from the *Delphineis* genus is the presence of an apical pore field in *Rhaphoneis* species (see Round *et al.*, 1990). A further possibility is that after a degree of dissolution has taken place, the diatom is misidentified as a raphe-less valve from the *Cocconeis* genus such as *Cocconeis scutellum*. The species is, however, recorded as a relatively common taxon from the Thames estuary by Juggins (1992) and from two North Sea coast estuaries by Horton (1997) but does not appear to be listed amongst common species in many other estuarine diatom studies. It appears preserve well in the subfossil but many valves showed signs of dissolution and it is possible that is does not preserve so well in older sediments. The variety in the distribution of *Rhaphoneis minutissima* within different Sites highlights the need for a broader geographical approach when developing modern analogue techniques with coastal diatoms to ensure certain taxa are not classified too narrowly.

Cymatosira belgica is often found in association with *Rhaphoneis minutissima,* mirroring its distribution across the transect but at a slightly lower relative abundance. This occurs at roughly 50% of the Sites and includes Aust, Blackwater, Bridgewater Bay, Burnham, Deben, Frampton, Gibraltar Point, Hamford Water, Mawddach, Sailor's Holme, Stiffkey and Wentloodge. *Cymatosira belgica* rarely occurs without *Rhaphoneis minutissima*, whereas

Rhaphoneis minutissima does occur as a significant species across some Sites without *Cymatosira belgica*, e.g. Alnmouth, Bowness, Caerlaverock, Lymington, Skyreburn Bay, Spurn Marsh, Welwick and Wigtown. Interestingly *Cymatosira belgica* is absent from all the Solway Firth Sites whilst *Rhaphoneis minutissima* does have a strong presence. This might suggest different tolerances in terms of latitude. There is clearly an association between the distribution of *Cymatosira belgica* and *Rhaphoneis minutissima* that warrants further investigation.

Some other widespread species include *Navicula perminuta*, *Navicula cincta*, *Navicula phyllepta*, *Navicula* sp. A, the *Achnanthes delicatula* complex and the *Navicula digitoradiata* complex. This habitat distribution is discussed in the following section.

Examining the diatom assemblages across each transect qualitatively by eye suggests certain local and some more widespread patterns in diatom distribution in relation to habitat and to elevation. It is also clear, however, that the taphonomic overprinting, whilst being an integral part of the character of any subfossil assemblage can only reduce the strength of the relationship between the diatom assemblage and variables such as elevation and habitat in any quantitative analysis. The widespread distribution of *Rhaphoneis minutissima* is a case in point, as is the random occurrence of significant levels of estuarine plankton such as *Paralia sulcata*, which is known to be a particularly robust species in terms of preservation in the fossil record (see section 5.3.5).

5.3.3 The diatom flora of intertidal habitats

Figure 5.7 shows a plot of species average abundance by habitat type for all species with an average abundance in any one habitat greater than 5%. An accompanying table with average abundance figures in given in Appendix 4. Figure 5.7 is useful for examining the general habitat patterns that appeared to be emerging in the description of the diatom assemblages at each Site. The results shown on this plot need to be interpreted with caution for two reasons. Firstly, because it plots species with an average abundance greater than 2, a number of taxa that are very rare but highly abundant at one or two Sites feature on the plot. Without this prior knowledge of their distribution across the Sites, they may appear to be a particularly significant characteristic of a certain habitat. A good example is *Navicula arenaria* which appears to be a distinguishing feature of the sandflat habitat, but as already discussed in sections 5.3.1 and 5.3.2.20, occurred a 67 % abundance in one sandflat Sample from Spurn

Point, thus greatly skewing its average abundance. Conversely, species that are found at a large number of Sites but at relatively low abundances will have a low average abundance and will therefore not feature on the plot, hence this diagram should only be used as an indication of characteristic assemblages for each habitat type. Secondly, some habitats are represented by only a handful of individual Samples, i.e. *Phragmites australis* beds, back saltmarsh, wet and dry pans. With fewer assemblages available to give a broader picture of diatoms found in these habitats, species that occur at high abundances in one Sample from one of these habitats will have an unusually high average abundance for that habitat; with this is mind absolute values for average abundances in these four environments will rarely be quoted in the following descriptive analysis although they are used to compare the other 7 habitats.

5.3.3.1 The saltmarsh and *Phragmites australis* beds

Starting at the higher end of the tidal range, the *Phragmites australis* and back saltmarsh, as suggested above, displays a relatively low species diversity in Figure 5.7 that is possibly due to the lower number of Samples collected from these habitats. They do, however, appear to be quite comparable in terms of diatom flora. This is not unexpected considering they occur at similar elevations and are also indicative or a fresher environment. Two species apparently indicative of these two habitats include *Navicula mutica* and *Nitzschia clausii*. Both of these habitats also share a number of common species with the other saltmarsh habitats, including species that are absent from or only present in low average abundances in intertidal flat habitats. These include *Nitzschia debilis, Navicula gregaria*, *Navicula cincta*, *Navicula digitoradiata* var. *minima* and *Denticula subtilis*, which all appear to be indicative of the saltmarsh and higher elevation environment. A number of these species had already suggested themselves as higher elevation species from the description of the individual Sites and it is interesting to see that *Navicula gregaria*, which appeared to have a variable distribution when taking the Sites individually, appears to have a stronger associated with the higher elevation environments than the lower ones, despite a constant presence throughout all.

The mid and low saltmarsh, as well as having a number of key taxa in common with the high elevation habitats, also display low abundances of species that occur as significant components of the intertidal flat assemblages; e.g. *Biremis lucens* and *Achnanthes delicatula* subsp. *hauckiana*. A subtle shift in the assemblage would appear to be occurring from higher saltmarsh through the mid and low saltmarsh down to the intertidal flats. *Navicula* sp. A

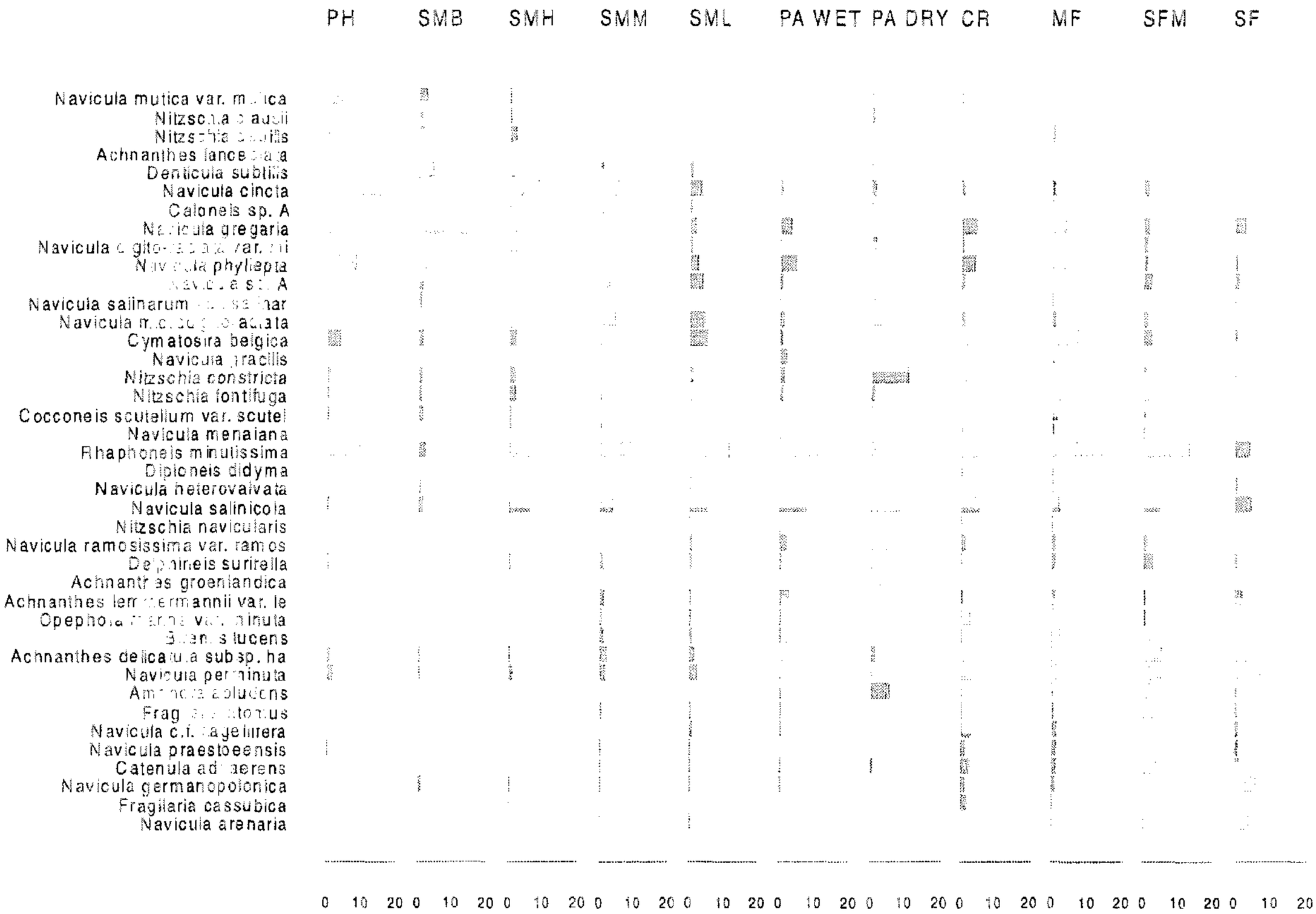


Figure 5.7 The distribution of selected diatom taxa across intertidal habitats

appears to be most strongly associated with the three main saltmarsh habitats (low medium and high) having an average abundance between 2.8% and 3.8% in these habitats but, with the exception of the muddy sandflat, less than 0.8% in all other habitats.

The association of *Navicula cincta* with saltmarsh environments is borne out by its habitat average abundance measurements, ranging from 3.4 on the low marsh to 10.9 and 9.5 on the mid and high marsh respectively. In the intertidal flats and creek habitats the average abundance of this taxon is consistently at or below 1.0% despite the unusually high count from the mudflat at Spurn Marsh.

5.3.3.2 Pans

The next two habitats plotted in Figure 5.7 are the wet and dry pans. These environments do not appear to show any specific trends or affinities with other habitat types. The Samples come from pans within a variety of other intertidal habitats, with a variety of sediment properties, and it is therefore not surprising that they show a very mixed flora with no species

emerging as having a strong association with the either wet or dry pans. There are, however, two features worth noting. Firstly that the wet pan assemblage, when compared to the dry pan assemblage, includes a number of species that appear at higher average abundances in the creeks and intertidal flats than the saltmarsh habitats. Secondly, *Navicula microdigitoradiata* appears to cluster around the centre of the plot across the pan and saltmarsh habitats.

5.3.3.3 Intertidal flats and creeks

The creek habitat in Figure 5.7 is similar to the intertidal flat habitats. This is because the base of most creeks tends to be more similar to the intertidal flats in terms of elevation, vegetation and sediment properties than the saltmarsh habitat they drain. There is a cluster of species plotting out on the bottom left of the diagram that are more indicative of the intertidal flats. They also have low average abundances in the wet pan and lower saltmarsh habitats. Species in this group include *Navicula perminuta*, *Biremis lucens*, *Achnanthes delicatula* subsp. *hauckiana*, *Navicula* c.f. *flagellifera*, *Navicula praestoeensis*, *Catenula adhaerens*, *Navicula germanopolonica* and *Fallacia cassubiae*. All these taxa were picked up from one or more Sites as being indicative of the sandflat assemblage along that particular transect. All of these taxa find their highest average abundance on the muddy sandflat except for *Navicula germanopolonica,* and *Navicula perminuta* which appear to be most strongly associated with the sandflat habitat, the former having an average abundance of 5.8%, well above that from the muddy sandflat at 1.3%. The mudflat habitat is distinguished from the muddy sandflat in having a lower average abundance of the species listed above and a predominance of *Navicula gregaria*, *Navicula phyllepta*, *Cymatosira belgica* and *Rhaphoneis minutissima*. None of these species are peculiar to the mudflat habitat, making the mudflat assemblage a relatively indistinct one in qualitative terms. It is possible that the distributions of a number of taxa that are found in abundance in the mudflat habitat are influenced by environmental variables other than habitat and elevation.

5.3.3.4 Cosmopolitan species

Whilst a number of species do occur at higher abundances in certain habitats, the overall picture of a gradient across the plot in Figure 5.7 from high to low elevation habitats is blurred somewhat by a number of species that are found in nearly all habitats, although some of these do show a pattern in their relative abundance between habitats.

Considering all habitats apart from the 4 with few Samples, *Rhaphoneis minutissima* reaches its highest average abundance in the mudflats at 17.9%, followed by the sandy mudflats at 12.9% and has its lowest average abundance in the sandflats at 8.9% (still a particularly high average when compared to other species distributions). Given that there are more Samples from the mudflat habitat than any other, this average is less likely to be pulled significantly by high or low outliers and, as tentatively mooted at points in the description of the individual Sites, it can therefore be suggested that, whilst *Rhaphoneis minutissima* is a species tolerant of a wide variety of estuarine conditions, it finds its optimum in the mudflat habitat, or at the very least in a finer grained substrate.

Some other species with a distribution across nearly all the habitats include *Navicula phyllepta*, *Cymatosira belgica*, *Navicula gregaria*, *Navicula perminuta*, *Navicula salinicola* and *Plagiogramma laeve*. *Cymatosira belgica* does follow the distribution of *Rhaphoneis minutissima*, with its highest average abundance in the mudflat habitat at 7.4% followed by the low and mid saltmarsh and having a similarly low average abundance on the sandflat at 0.2%. *Navicula gregaria* has already been discussed in section 5.3.3.1. Although *Navicula perminuta* occurs frequently across all habitats it peaks in average abundance on the sandflat at 7.2% followed by the neighbouring habitat of sandy mudflat (5.0%) and often similar habitat of the creeks (3.2%), supporting the conclusions drawn so far that this is a characteristic sandflat taxa. Excluding the four habitats with a low number of Samples, *Navicula phyllepta* has its highest average abundance on the mudflat at 4.9% and its lowest on the sandflat at 0.3% but in general it does not appear to show any particular habitat preference apart from a general absence from the sandier low elevation habitats suggesting that sediment properties rather than elevation or habitat may be more important in controlling this species distribution. *Navicula salinicola* appears to be a truly adaptable euryhaline estuarine diatom, less likely to be found in the fresher habitats at the very top of the tidal range. Likewise, no specific pattern can be discerned from the habitat distribution of *Plagiogramma laeve*. It peaks in average abundance in the back saltmarsh at 3.5%. This could suggest a habitat, elevation or salinity preference, but the next two highest average abundances are from two quite dissimilar environments, the high saltmarsh and muddy sandflat, making it difficult to draw any conclusions other than this being, like *Navicula salinicola* a very adaptable species, or that this species' record has a large degree of taphonomic overprinting.

Nitzschia constricta and Nitzschia fontifuga occur at low abundances across all habitats. *Nitzschia* is an epipelic genus so this lack of affinity with the intertidal mudflats is probably due to tidal redistribution of the taxa.

One group of diatoms conspicuous by their absence from Figure 5.7 are the centric estuarine planktonic forms such as *Actinocyclus senarius*, *Thalassiosira* species and *Paralia sulcata*. Their low average abundance in any one habitat but high N_2 diversity overall shows how, as the assemblage looses some of the finer silicified taxa, these more robust centric forms may come to dominate in the assemblage incorporated into the fossil record.

5.3.4 The diatom flora of salinity classes

Figure 5.8 Shows diatom species average abundance within the four salinity classes represented in the dataset; oligohaline, mesohaline, polyhaline and euhaline (for species with an average abundance in any one salinity class greater than 1%). The small number of true fresh species shown (oligohaline) is likely to be due to the fact that the estuarine environment, by it nature, does not provide condition suitable for most oligohaline forms due to the need to be able to adapt to at least some degree of salinity fluctuation, even high up an estuary where the tidal waters are greatly diluted.

Navicula cincta and *Navicula gregaria* are clearly adapted to lower salinity habitats, peaking in average abundance in the oligohaline class and falling dramatically across the increasing salinities classes. The vast majority of the species, however, do not appear to show any particularly strong salinity preference, especially *Cymatosira belgica*, *Rhaphoneis minutissima*, *Navicula phyllepta* and *Navicula salinicola* all having high average abundances in each salinity class. This cluster of high abundance species around the centre of the plot does, however mask the more subtle trends in some of the lower abundance species with all the taxa listed below *Navicula salinicola* showing an increasing abundance with increasing salinity up to the polyhaline, with a few species increasing again into the euhaline class Species showing this more subtle salinity gradient include *Navicula microdigitoradiata*, *Nitzschia dissipata*, *Navicula* sp. A., whilst *Nitzschia fontifuga*, *Amphora* c.f. *delicatissima*, *Nitzschia coarctata*, *Navicula ramosissima* and *Navicula meniscus* all show a marked preference for high salinity habitats, namely the polyhaline and euhaline classes. Above *Cymatosira belgica* we see a group of species with broad salinity tolerance but with higher average abundances in the mesohaline and polyhaline salinity classes marking them out as

true estuarine brackish forms. This group includes *Navicula perminuta*, *Biremis lucens*, *Achnanthes delicatula* subsp. *hauckiana*, *Plagiogramma leave*, *Catenula adhaerens* and *Navicula germanopolonica*.

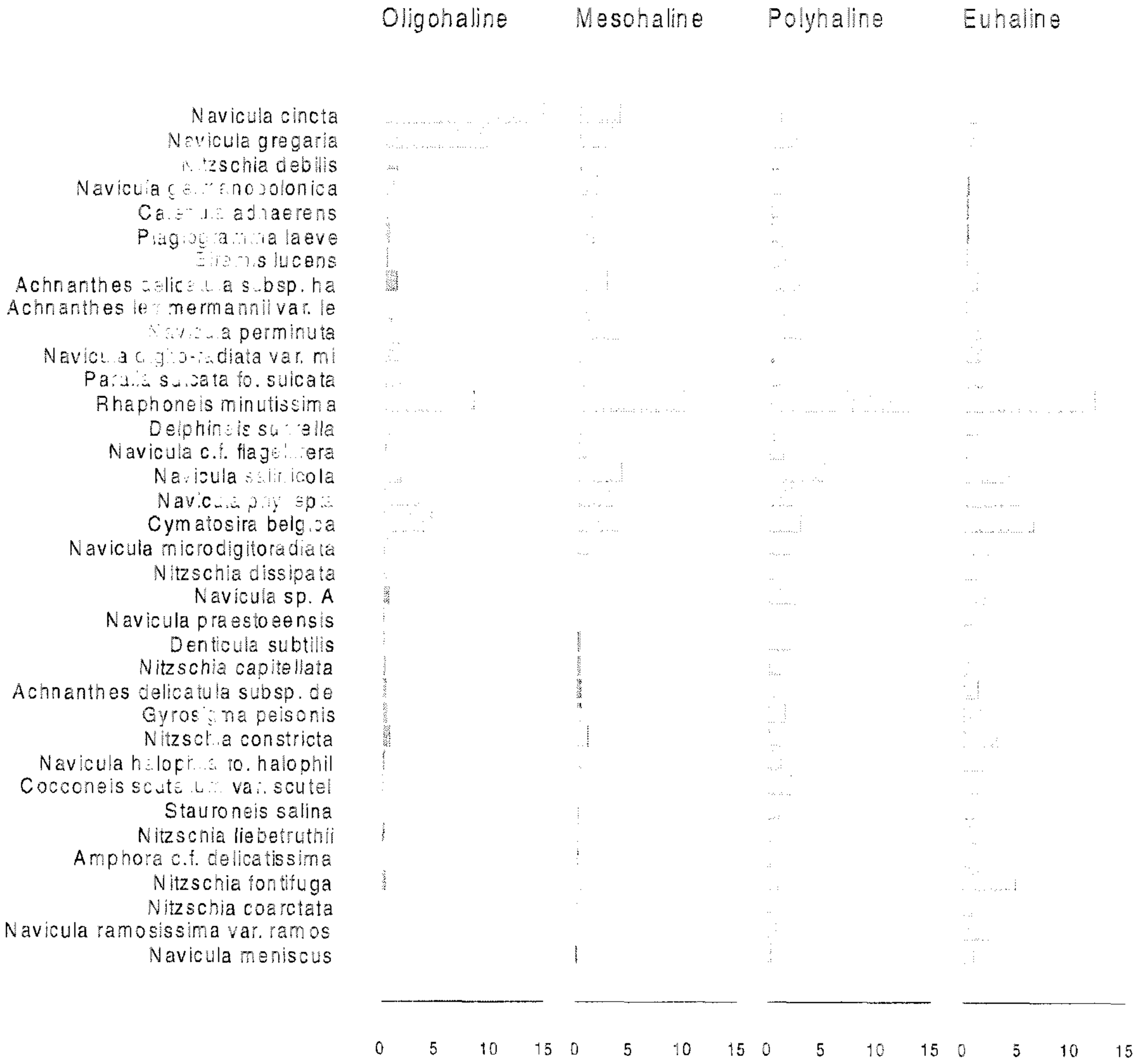


Figure 5.8 The distribution of selected diatom taxa across salinity classes

5.3.5 Paralia sulcata

Before continuing with the analysis of the data one species deserves some early attention. In the preceding section *Paralia sulcata* has been classed as an estuarine planktonic form. This categorisation requires some justification because of the debate within the literature on

the autecology of this species, not least because it often occurs at high abundances in estuarine subfossil and fossil diatom assemblages (e.g. Hemphill-Haley, 1995a; Zong 1997a).

Paralia sulcata is a robust, centric, chain-forming diatom that has been variously classified as benthic (from muddy estuaries), epiphytic and planktonic from a variety of salinity class habitats. The different life forms and ecological preferences published for this species are summarised by Zong (1997a) revealing evidence for a benthic and planktonic life-form. Zong (1997a) analyses the changing abundance of *Paralia sulcata* through the sediment record from eight northwest Scotland isolation basins. This analysis is used to suggest an autecology adapted to warmer waters, greatly varied salinity, a minimum water depth of > 1 m and fine-grained organic enriched sediment (Zong, 1997a). Cooper (1995) suggests that *Paralia sulcata* might drift along the bottom of coastal waters with a community of unattached bottom dwelling diatoms (Zong, 1997a). But Zong's (1997a) study does not favour this hypothesis as it occurs in isolation basin in too high and consistent an abundance to be brought in on occasional high tides and is therefore concluded to be autochthonous to the isolation basins.

These ecological preferences proposed by Zong (1997a) are shown to agree with a number of other authors. The data in this study puts *Paralia sulcata* at its highest average abundances per habitat in the mid saltmarsh, creek and mudflat with its lowest in the sandflat (see Appendix 4), although statistically there is no significant relationship between its distribution over habitats and the tidal gradient (see section 6.3.5). In terms of salinity preference, *Paralia sulcata* is found in roughly equivalent abundance in oligohaline, mesohaline and polyhaline Samples (see Figure 5.8). This would appear to agree with the suggestion that *Paralia sulcata* favours fine-grained sediments and has a wide salinity tolerance. This might be thought to be an admission of an assumption that *Paralia sulcata* is an intertidal benthic species, but it could also be a reflection of the fact that *Paralia sulcata* thrives in waters of low light (Conover, 1956), which would be a more prominent characteristic of estuaries with large amounts of fine-grained sediment as this increases turbidity.

The lack of any significant relationship between *Paralia sulcata* and intertidal habitats or intertidal elevation and low but common abundances in numerous samples suggests a species that is allochthonous to the intertidal habitat, but autochthonous to a nearby habitat. Given the conclusion in Zong (1997a), supported by other authors, that *Paralia sulcata* has a minimum water depth tolerance of 1 m it would appear most likely that this species occurs in the subtidal zone of the estuary and is brought up into the intertidal zone by the movement of

the tides. The chain-forming character of this species means that a small number of chains in a Sample can lead to a high abundance of diatom valves. It is not possible, from the data collected in this study, to determine whether *Paralia sulcata* is indeed a member of the subtidal benthos, or the estuarine plankton. For the purposes of this study it is categorised as estuarine plankton on the grounds that its distribution is more similar to other plankton forms such as *Thalassiosira* species (see section 6.3.5) than to species derived from the subtidal benthic habitat such as the epiphytic and epipsammic *Cocconeis* forms (see section 6.3.4).

5.4 Cluster analysis of the diatom assemblages

Following the descriptive analysis of the diatom distributions in section 5.3, groupings in the 116 diatom Samples are identified using TWINSPAN. The output of the TWINSPAN cluster analysis is displayed in Appendix 5. Abundance weightings were used to give more importance to the higher abundance pseudospecies cut levels; the weighted abundance cut-off levels are indicated at the bottom of the TWINSPAN table in Appendix 5.

After analysis of the groupings at difference hierarchical levels, a total of 9 groups were distinguished from the diatom dataset. A summary of the diatom species distribution across these 9 TWINSPAN groups is show in Figure 5.9, showing the mean abundances of taxa within each Group. The characteristics of these groups are described in turn in terms of floristic composition and in relationship to the environmental variables of habitat (shown in Table 5.6), salinity (shown in Table 5.7), normalised tidal height and sediment properties of grain size and LOI (all shown in Figure 5.10). The caution given in section 4.6.2 relating to the method of group division must be kept in mind when analysing the groups. They are therefore not forced into indicating particular ecological conditions where no specific association is apparent. The impact of high abundance cosmopolitan species discussed in section 5.3.3.4 must also be kept in mind.

5.4.1 Group One

On initial inspection it is clear that the main species in Group One are those plotting out in the upper middle section of the TWINSPAN diagram (Appendix 5), also seen clearly in the top left of Figure 5.9. These include taxa with relatively high abundances over a number of Groups such as *Rhaphoneis minutissima* (RA007A) and *Cymatosira belgica* (CT001A) and others with lower abundance but still with widespread occurrence across a number of Groups,

such as *Paralia sulcata* and *Actinocyclus senarius* (AT001A). Species that distinguish this Group from Group Two (both Groups being subdivisions of the same larger Group) are the occurrence of *Navicula cincta* (NA021A) consistently and at a high abundance, and the occurrence of *Gyrosigma peisonis* (GY021A) and *Gyrosigma eximuim* (GY014A). This Group also has as a generally lower abundance of the more cosmopolitan taxa, mentioned above, compared to Group Two.

In terms of habitat this is quite a mixed Group with two Samples from each of the low saltmarsh, mid saltmarsh and *Phragmites australis* habitats (see Table 5.6) but in terms of salinity four of the three are oligohaline environments and two mesohaline, pointing to a lower salinity preference for this Group (see Table 5.7). In terms of sediment properties this Group has a high silt content, a moderate clay content and a distinctly low sand content pointing to a finer grained habitat (see figure 5.10). The normalised tidal height is the highest

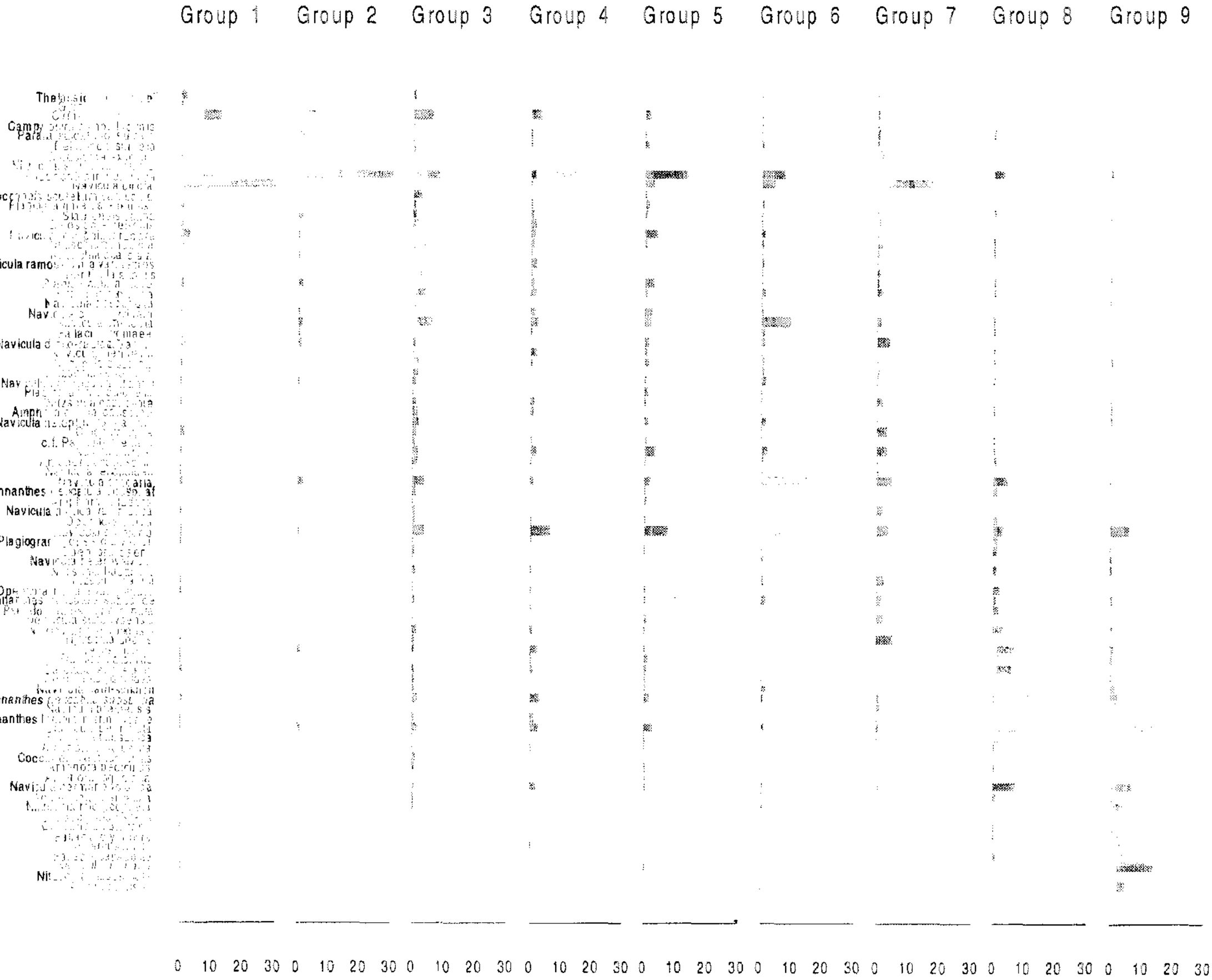


Figure 5.9 Diatom species distribution across the nine TWINSPAN groups

Table 5.6 Distribution of Samples within 9 TWINSPAN group by habitat type

Habitat	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9
Sandflat	0	0	0	0	4	0	0	4	5
Muddy sandflat	0	0	1	0	4	0	0	2	0
Mudflat	0	7	8	4	3	2	1	2	0
Creek	0	0	3	0	2	0	0	2	0
Wet pan	0	0	0	2	1	1	0	1	0
Dry pan	0	0	1	0	0	1	0	0	0
Low saltmarsh	2	1	3	6	6	1	0	0	0
Mid saltmarsh	2	0	2	0	3	0	3	1	0
High saltmarsh	0	1	4	0	2	4	5	0	0
Back of saltmarsh	0	0	1	0	4	2	0	0	0
Phragmites australis beds	2	0	1	0	0	1	1	0	0

Table 5.7 Distribution of Samples within 9 TWINSPAN group by salinity class

Salinity Class	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9
Euhaline	0	0	6	0	1	0	1	0	0
Mesohaline	2	7	8	6	18	6	7	8	5
Oligohaline	4	1	0	0	0	4	1	1	0
Polyhaline	0	1	10	6	7	2	1	3	0

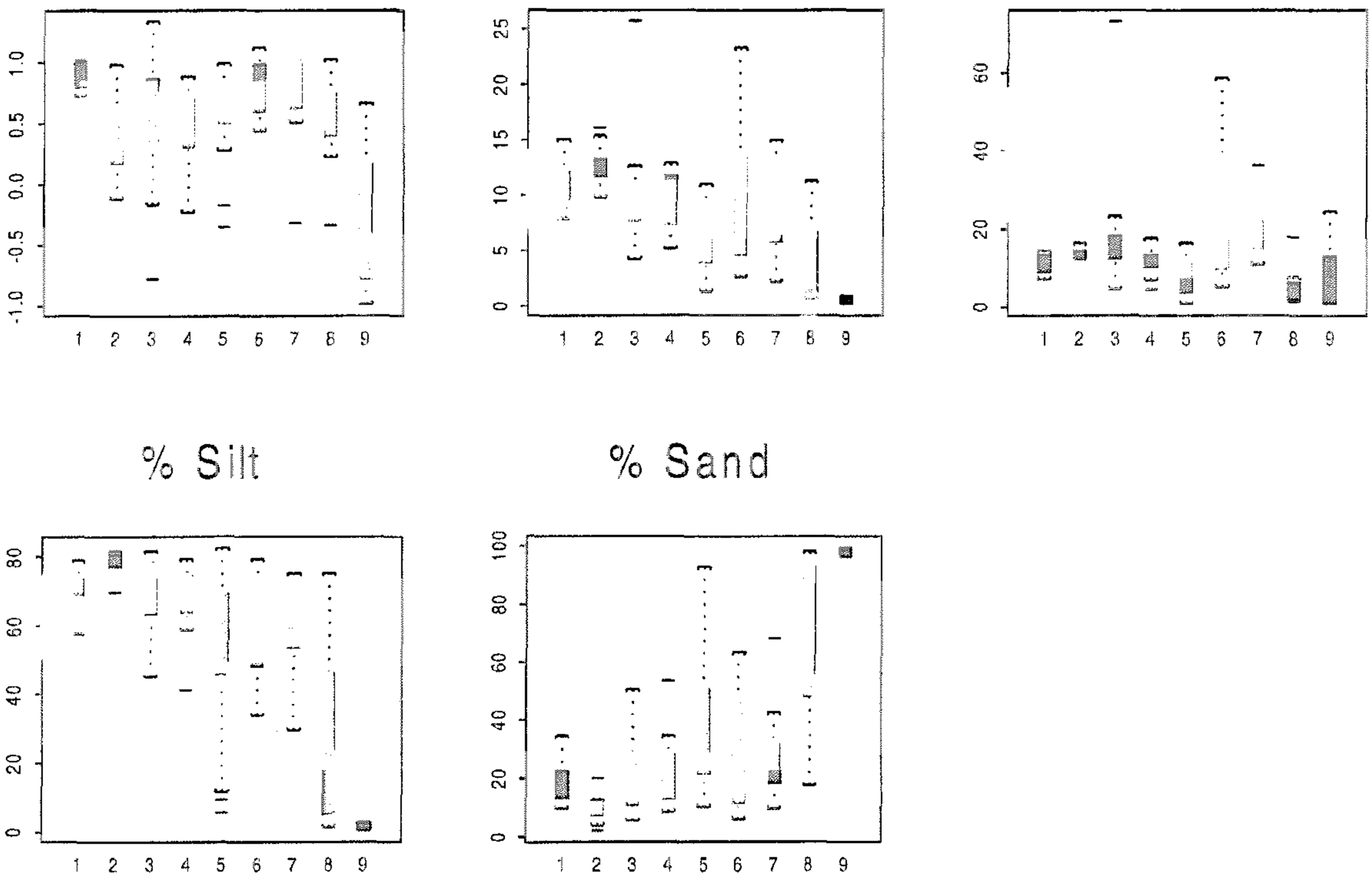


Figure 5.10 Boxplots showing the distribution of TWINSPAN Groups over, normalised tidal height and sediment properties of grain size and LOI

of any Group visibly indicating a higher elevation preference. This is in keeping with the two *Phragmites australis* habitats features in this Group but is rather unexpected for the other four mid and low saltmarsh Samples. These saltmarsh Samples, whilst having a habitat indicative of the low and mid saltmarsh must be closer in elevation to the height at which high saltmarsh communities are more commonly found. Four of the six Samples come from the Severn estuary, also suggesting a degree of regionality in this Group.

In general terms this Group appears to be one from higher elevation lower salinity habitats with a certain degree of regional bias towards the Severn estuary and is the most indicative of *Phragmites australis* beds of any of the Groups (although this should not relied upon too heavily given the low number of *Phragmites australis* Samples in the dataset). Indicative taxa include *Gyrosigma* species and high levels of *Navicula cincta*.

5.4.2 Group Two

Diatom species most abundant and consistently present across this Group include *Rhaphoneis minutissima* (RA007A);*Campylosira cymbelliformis* (CPS02A), *Cymatosira belgica* (CT001A), *Paralia sulcata* (PA001A), *Delphineis surirella* (DEL01A), *Thalassiosira oestrupii* (TH026A) and *Plagiogramm brockmanii* (PR011A); an interesting mix of intertidal benthos and estuarine plankton (see Figure 5.9). Table 5.6 shows that 7 of 9 Samples in this Group come from the mudflat habitat, a strong indication of the habitat preference of this Group. Abundances of *Rhaphoneis minutissima* and *Cymatosira belgica* support this. The Samples from this Group are predominantly mesohaline environments.

This Group has the lowest sand content and highest clay and silt content with the some of the smallest inter-quartile ranges for the sediment properties of any of the Groups (see Figure 5.10). This lack of spread in the grain size data for this Group points to a close association with the silty mudflat habitat, supported by the low normalised tidal height. The full inter-quartile range for the normalised tidal height falls above ML, but this does not conflict with the assumptions so far that this is a mudflat habitat as ML usually falls within the intertidal flats, MHWN marking the point where pioneer vegetation often begins to establish its self.

Eight of the nine Samples come from the Severn estuary, an even stronger regional association than Group One. Given that Group One and Group Two are subdivisions of the same higher Group it is reasonable to assume that the higher Group from which they are taken is, above all, a fine-grained Severn estuary grouping, subdividing into higher and lower elevation habitats.

5.4.3 Group Three

Group Three is a large Group containing 21 Samples, only exceeded in size by Group 5. Although TWINSPAN analysis suggests a number of subdivisions to this Group, none of them appear to follow any particular ecological pattern so the division was not taken any further. There are number of diatoms that appear in most Samples across this Group and occur more frequently in this Group than any others, these are *Gyrosigma distortum* (GY013B), *Cocconies neodimunata* (XXX477), *Nitzschia compressa* (NI200A), *Campylosira cymbelliformis* (CAS02A), *Navicula pavillardii* (NA559A) *Paralia sulcata* (PA001A) and *Nitzschia coarctata* (XXX914). Species that occur frequently in this Group and often at

relatively high weighted abundances, but also feature strongly in one or more other Groups include *Navicula ramosissima* (NA059A), *Navicula phyllepta* (NA058A), *Rhaphoneis minutissima* (RA007A), *Cymatosira belgica* (CY001A) and *Navicula salinicola* (NA614A), seen clearly in Figure 5.9. *Achnanthes delicatula* subsp. *hauckiana* (AC016C) and *Navicula perminuta* (NA565A) feature permanently in this group but are also frequent in other Groups at high abundances. Species that find their most frequent occurrence and highest abundances in Group Three are few, considering the size of the Group; they include *Gyrosigma peisonis* (GY021A) *Cocconeis scutellum* (CO007A), *Nitzschia fontifuga* (XXX391), *Nitzschia constricta* (NI083A) *Amphora* c.f. *delicatula* (XXX550) and *Denticula subtilis* (XXX649). This is not, therefore, a Group whose ecological affinities are evident from the dominant and frequently occurring diatom taxa although the presence of *Denticula subtilis* at its highest abundances suggests some higher elevation habitats within this Group.

Examining the habitat distribution in Table 5.6 for the Samples in Group Three sheds a little extra light on this Group. One third of the Samples are from the mudflat habitat and another third come from the neighbouring or nearby habitats of creeks, low and mid saltmarsh. Of the remaining third of the Samples, half of them come from the high saltmarsh with the rest distributed over all the remaining habitats. In terms of habitat, mudflat, creeks and saltmarsh are most important. The normalised tidal range in Figure 5.10 supports this with an inter-quartile range bridging MLWN and the upper and lower adjacent values spanning from below ML to above MHWS. Similar to Groups One and Two, this third Group has low sand content and high silt content with a moderate range of clay in relation to other Groups (see Figure 5.10). The Group also has one of the higher LOI ranges. The Group also spans the mesohaline, polyhaline and euhaline Groups (Table 5.7) with two thirds of the Samples falling within the polyhaline and euhaline categories, thus this Group would appear to cluster more around the higher salinity ranges. There is little in terms of firm conclusions that can be draw about the ecological character of this Group.

All bar 4 of the 21 Samples come from southern East Anglia and the south coast of England. Group Three would therefore appear to be a southern British Group from silty habitats of higher than average salinity range.

5.4.4 Group Four

There are a large number of species with frequent and often abundant occurrences in Group Four but no species stand out as having a particularly higher abundance in this Group compared to any of the others, many of them being quite cosmopolitan species. Species that are common in this Group but also occur frequently in others include *Navicula ramosissima* (NA059A), *Nitzschia fontifuga* (XXX391) *Navicula phyllepta* (NA058A), *Plagiogramma leave* (PR005A), *Navicula* c.f. *flagellifera* (XXX396), *Gyrosigma peisonis* (GY021A), *Rhaphoneis minutissima* (RA007A), *Cymatosira belgica* (CA001A), *Amphora* c.f. *delicatissima* (XXX550), *Navicula salinicola* (NA614A), *Achnanthes lemmermanii* (AC047A), *Navicula praestoeensis* (XXX652), *Achnanthes delicatula* subsp. *hauckiana* (AC016C) *Fragilaria pinnata* (FR001A) and *Navicula perminuta* (NA565A) (see Appendix 5 and Figure 5.9). Species with the highest abundance within the Group include *Rhaphoneis minutissima, Cymatosira belgica, Navicula salinicola, Navicula praestoeensis* and *Achnanthes delicatula* subsp. *hauckiana. Rhaphoneis minutissima* exhibits its second highest overall levels of abundance in this Group, after Group Two, the Severn estuary mudflat Group.

The Samples in Group Four come from habitats around MHWN, with a similar but slightly lower range to Group Three. The specific habitats, shown in Table 5.6, include 4 mudflat Samples, 6 low saltmarsh Samples and 2 wet pan Samples (both from the mid to low saltmarsh). Group Four has a tidal height just above Group Two and Group Nine, mudflat and sandflat Groups respectively (see Figure 5.10). This agrees with the habitat distribution of Group Four. The diversity of common species in this Group listed above reflects the plot of species average abundance by habitat type in Figure 5.10, which suggested a strong degree of overlap of low saltmarsh taxa with higher and lower elevation communities. The sediment grain size properties of this Group, in Figure 5.10, are very similar to Group Three with a generally high silt content and moderate clay content; this could account for Groups Three and Four being divisions of the same higher grouping. The salinity classes of the Group Four Samples are distributed with 50% as mesohaline and 50% polyhaline indicating a preference for the mid to upper salinity ranges, again not too dissimilar to Group Three (see Table 5.7).

All bar one Sample in this Group come from the mid North Sea coast, from the Humber, Wash and the North Norfolk Coast giving Group Four a strong east coast identity.

5.4.5 Group Five

Group Five is the largest cluster containing 26 Samples. The TWINSPAN plot does suggest three subdivisions of this Group but, in terms of diatom flora, the divisions seem to be centred around elevated abundances of a few taxa at the left hand side of the Group in Appendix 5 (*Fragilaria atomus* (FR025A), *Navicula microdigitoradiata* (XXX928), *Navicula cincta* (NA021A) and *Navicula* sp. A (XXX643) but these are not considered sufficient to justify a separate ecological grouping. Furthermore, when examining the geographical source of the Samples within this large Group it is clear that the three suggested sub-divisions essentially split the Group into three regional groupings, one from the Wash on the left of the Group, one from the Solway Firth in the centre and the other, on the right hand side, a mixed Group dominated by Sites from the more northerly end of the study area. For the purposes of this study it is more relevant to look for other ecological characteristics such as sediment properties, tidal height and habitat within the cluster, hence its retention as one large group.

The diatom flora, as might be expected in such a large Group is very diverse but there are some particularly abundant taxa that stand out in Figure 5.9. Common and abundant taxa throughout the Group include *Navicula perminuta* (NA565A), *Navicula salinicola* (NA614A), *Navicula gregaria* (NA023A), *Navicula cincta* (NA012A), *Rhaphoneis minutissima* (RH007A), *Navicula phyllepta* (NA058A) and *Navicula* sp. A (XXX643). This is quite a mixture in terms of the conditions each individual species, at this stage in the analysis, might suggest.

This Group has the broadest habitat distribution with two or more Samples from the creek, mudflat, sandflat, muddy sandflat, high mid and low saltmarsh habitats, however low saltmarsh, sandflat and muddy sandflat account for over 50% of the Samples (see Table 5.6). Considering the number of sandflat and muddy sandflat Samples it is perhaps surprising that the normalised tidal height range of this Group shown in Figure 5.10 is within the higher portion of tidal range between ML and MHWS but despite the variety in habitat types the normalised tidal range of this Group is comparatively distinct. The sand and muddy sandflat Samples must come from the upper parts of the intertidal flats close to pioneer saltmarsh inception. Of all the Groups, Group Five has the least extreme grain size characteristics having a more even mix of clay, silt and sand than any other Group but still dominated by silt, as seen in Figure 5.10.

Over two thirds of the Samples are classified as mesohaline which is the largest salinity range of any of the salinity classes (see Table 5.7). Overall, therefore, Group Five is the least ecologically distinct of all the TWINSPAN Groups with a high variety of habitats and diatom species present; it could be called a general upper intertidal estuarine Group subdivided by more regionally distinctive floras.

5.4.6 Group Six

Group six and seven to not separate from one another until the fifth level of Group divisions in the TWINSPAN diagram (the penultimate division). Nonetheless they do appear to be distinct from each other in ecological terms. Group Seven has a very strong identity, as discussed in the next section and Group Six, although not perhaps quite so distinct, does appear to have its own unique ecological characteristics.

Diatom species indicative of this Group by their frequency of occurrence and, or, abundance include most especially *Navicula salinicola* (NA614A), *Navicula gregaria* (NA023A) and *Navicula phyllepta*, but also *Navicula cincta* (NA012A) and *Rhaphoneis minutissima* (RA007A) (see Figure 5.9). Species common at low abundances include *Nitzschia fontifuga* (XXX391), *Navicula flanatica* (NA363B), *Nitzschia constricta* (NI083A) *Navicula microdigitoradiata* (XXX928), *Navicula halophila* (NA022A) *Achnanthes minutissima* (AC013A), *Nitzschia dissipata* (NI015A), *Navicula paul-schulzii* (XXX699) and *Navicula perminuta* (NA565A).

Group Six together with Group Seven and Group One have the highest normalised tidal height ranges in Figure 5.10. Group Six has a very similar range to Group Seven, the main difference being slightly higher and slightly lower upper and lower adjacent values respectively. This reflects the different distribution of habitats within Group Six in Table 5.6, the largest number coming from the high saltmarsh but three higher habitats (two back saltmarsh and one *Phragmites australis* bed) pulling up the normalised tidal height range, and two mudflat Samples pulling down the lower adjacent value. In habitat and elevation terms Group Six appears to be a high saltmarsh and transitional (to terrestrial) habitat Group at the upper end of the tidal range. The salinity classes of the Samples fit with this description, with 2 polyhaline, 4 oligohaline and 6 mesohaline Samples in Table 5.7. Sites predominantly from the higher extreme of the tidal range can experience high salinities due to the elevated salinity of the occasional flood tide waters through evaporation, or fresher conditions at the very top

of the range due to the dominance of the freshwater surface runoff and precipitation. The wet and dry pan Samples present in this Group come from within the higher saltmarsh and hence fit with this delineation of the Groups ecological characteristics, but the presence of the two mudflat Samples makes the character of this Group a little less tight than that of Group Seven, its closest counterpart. Group Six and Seven also have the highest LOI ranges, although Group Six's range is significantly broader than Group Seven. Higher LOI values would be expected from a group predominantly consisting of higher elevation habitats as vegetation and tidal-rafted debris accumulate on the substrate.

The geographical location of the Samples within the study area is widespread removing any regional bias from the Group.

5.4.7 Group Seven

Species occurring frequently and often or always at high abundances in this Group include *Navicula salinicola*, *Navicula gregaria*, *Navicula cincta*, *Rhaphoneis minutissima*, *Navicula* sp. A, *Nitzschia debilis* and *Navicula mutica* shown in Figure 5.9. Together these species, from the results of the descriptive analysis, strongly suggest a saltmarsh community and the ecological characteristics of this Group bear this out, as discussed below. Species indicative of the upper saltmarsh by their absence from this Group in any number include *Navicula perminuta* and *Cymatosira belgica*.

This Group is clearly a saltmarsh grouping from above the pioneer marsh zone with high normalised tidal heights (Figure 5.10). Furthermore, Table 5.6 reveals that 5 of the 10 Samples in the Group come from the high saltmarsh with a further 3 from the mid saltmarsh. In salinity terms this is another generally mesohaline Group (see Table 5.7). All the Samples come from North Sea Sites narrowing the character of the cluster down further to being a North Sea upper saltmarsh grouping.

5.4.8 Group Eight

Group eight exhibits a strong clustering of abundant taxa to the bottom of the TWINSPAN plot in Appendix 5 and Figure 5.9. This Group is less diverse than some of the earlier Groups described and the dominant taxa feature at particularly high abundances. These include (Figure 5.9) *Navicula perminuta*, *Navicula germanopolonica*, *Achnanthes delicatula* subsp.

hauckiana, *Navicula praestoeensis* and *Achnanthes lemmermannii*, followed by species with a more variable presence including *Rhaphoneis minutissima*, *Navicula salinicola*, *Navicula gregaria* and *Opephora marina* var *minuta*. Frequent species occurring at lower abundances include *Opephora olsenii*, *Nitzschia frustulum* and *Cocconeis peltoides*.

Collectively the above group of species point strongly to an intertidal flat assemblage and the habitat distribution of Samples within Group Eight support this. The 11 Samples in this Group are spread across the creek, mudflat, muddy sandflat and sandflat habitats, with one unusual Sample from the mid saltmarsh in Table 5.6. The Group has a strong identity as an intertidal flat Group, creeks naturally aligning with the major intertidal flat habitats for reasons already discussed. The collective sediment properties of this Group further support the mixed intertidal flat character having conspicuously lower slit and higher sand content than all but Group Nine (see Figure 5.10). The broad inter-quartile range of the sand and silt component reflects the variety of sediment types found on the intertidal flats from coarse sandflats to fine silty mudflats. This group has the lowest median and inter-quartile range for LOI suggesting a lack of higher vegetation and large degree of tidal scouring in keeping with the characteristic of open intertidal flats. Given the clear habitat association of this Group it is somewhat unexpected that its normalised tidal height range, whilst being in the lower four of the nine Groups, is higher than Group Four, identified as a mudflat and low saltmarsh Group (see Figure 5.10). Having said this, the elevation of the mid saltmarsh Sample is responsible for pulling up the upper adjacent value length plus creeks and un-vegetated flats can extend at least up to MHWN, significantly above ML. In salinity terms Table 5.7 Shows the Group to be predominantly mesohaline with a few polyhaline Samples, similar to the mudflat cluster in Group Two.

The strong intertidal flats nature of this Group is further strengthened by the fact that the Samples are completely mixed in terms of geographical source.

5.4.9 Group Nine

Group Nine is the most distinctive diatom Group, see clearly in Figure 5.9 and, in keeping with the distinctiveness of this environment throughout the descriptive analysis, this Group appears to be a low elevation sandflat grouping. Significantly high abundance taxa include *Navicula perminuta* (NA565A) and *Navicula germanopolonica* with a noticeably absence, or particularly low abundance, of *Rhaphoneis minutissima* and *Cymatosira belgica*. *Navicula*

perminuta does have a significant presence in other Groups too, but this is to be expected given the wide-ranging distribution of this species across the habitats, illustrated in Figure 5.7. The Group also contains a distinct cluster of *Cocconeis* species (*neothumensis, distans* and *hoffmanii*) with *Amphora wiseii* and *Fallacia cassubiae*, all species already identified as characteristic of sandflat assemblages. There is also a distinct lack of species plotting out towards the middle and top of the TWINSPAN diagram, already identified as being saltmarsh and mudflat taxa. Other obvious signs are the high weighted abundance values towards the very bottom of the plot for *Navicula arenaria* (NA220A), known to come from the sandflats at Spurn Point, and the consistent occurrence and high abundance values for *Fragilaria schulzii* also from the sandflats at Spurn Point.

Table 5.6 reveals that the Samples in Group nine are all from a sandflat habitat. All Samples in this Group are categorised as mesohaline in terms of salinity in Table 5.7. Group Nine also has the lowest normalised tidal height in Figure 5.10; strikingly lower than all other Groups and predominantly below ML, although it also has a large inter-quartile range. Group Nine also stands out in stark contrast to the other Groups in its very low clay and silt content and extremely high sand content, all Samples being over 90 % sand. The sediment property of LOI has a low inter-quartile range but a range that extends to higher percentages of LOI than Group Eight. All together these results point to a Group strongly associated with the sandflats below ML.

5.4.10 Summary of the diatom TWINSPAN Groups

A summary of the ecological characteristics of each of the nine TWINSPAN Groups is given in Table 5.8. The column showing strength of ecological explanation is purely subjective based on the apparent strength of association between the Group and defining environmental variables and is therefore simply a guide to interpretation. Most of the TWINSPAN Groups do appear to have a degree of ecological distinctiveness, some much more so than others. The Group that is least distinctive in ecological term is Group Five and Group Three also has a weaker association than many other Groups. These are the largest two Groups so a degree of homogenisation is perhaps not surprising and it is important not to force them into to subdivisions that do not make any sense in terms of environmental variables. Coastal diatom assemblages are by their nature noisier than inland freshwater assemblages so a strong ecological explanation emerging for five of the nine Groups (Two, Six, Seven, Eight and Nine) and a general ecological character for three more (One, Three and Four) is an

Table 5.8 Summary of the ecological characteristics of the 9 TWINSPAN Groups

TWINSPAN Group	Strength of ecological explanation	Major ecological characteristics	Regionality
One	Moderate	High elevation, low salinity, silty habitats	A Severn estuary bias
Two	Strong	Mudflats above ML	Severn estuary
Three	Moderate	Silty mudflat and saltmarsh assemblage from higher salinity habitats	Southern Britain
Four	Moderate	Mudflat and low/pioneer saltmarsh	Mid North Sea coast
Five	Weak	No specific defining character, a general mid-tidal range brackish group with mixed sediment properties	Mixed, with three regional groupings within
Six	Strong	High marsh and upper transitional habitats, mixed salinity although predominantly lower salinity	Mixed
Seven	Strong	Saltmarsh assemblage around and just below MHWS	North Sea Coast
Eight	Strong	Intertidal flats assemblage from around and below MHWN	Mixed
Nine	Strong	Sandflat assemblage from below ML	Mixed

encouraging result. The apparent influence of regionality in the division of a number of the Groups also puts the strength of the ecological character exhibited in a fairer light as they are still apparent despite a strong regional association in some Groups. Zong and Horton (1999), in a similar study employing diatom assemblages from 6 intertidal environments in Britain, also found a certain degree of variation in the diatom flora at different sites. As this regionality in diatom flora is picked up in a study including six sites, it is not surprising that it

also picked up in this study with 25 sites over a larger geographical area. Zong and Horton (1999) go on to suggest that the between-sites differences in diatom flora reflect the differences in the environmental variables of substrate, tidal regime, salinity and ground-water acidity. The known large degree of variety within this study's training dataset for the first three of these variables would suggest that the effects of regional and local differences in these variables can only add to the degree of variety in the composition of the diatom flora.

Habitats that come out with a distinctive diatom flora associated with them include low sandflats, saltmarsh, higher saltmarsh and upper transitional habitats, intertidal flats and mudflats. The distinctive mudflat assemblage, Group Two, cannot be taken as indicative of mudflats throughout the study area due to its strong regional association with the Severn estuary. The same can be said of Group Seven, which should not be taken as indicative of saltmarsh habitats throughout the study area but can be taken as such for the North Sea coast. The habitats coming out with most distinctive clusters in the TWINSPAN analysis are all relatively high or low in term of the tidal gradient. More central transitional communities within the intertidal habitat succession have less distinctive diatom and ecological characteristics in the TWINSPAN analysis, these being Groups Three, Four and Five, reflecting these mid-successional habitats tendency to have a less distinctive, more mixed flora. Zong and Horton (1999) also found this to be the case for low and mid saltmarsh assemblages. Group One is the most unique in character being more strongly defined by low salinity Samples than any of the other groupings, with Samples from the Severn and the Wash.

An interesting feature of the TWINSPAN Groups' ecological characteristics is a lack of any distinctive pattern emerging for the LOI data, beyond a weak pattern of higher elevation Groupings having slightly higher LOI (see Figure 5.10). This lack of distinctiveness in this particular sediment property relationship is surprising as Horton (1997) shows a close relationship between elevation and LOI.

Some of the species considered through this Chapter are beginning to show some more or less distinctive ecological preferences within the estuarine intertidal environment and these relationships are explored further in the Chapter Six. What is already clear, however, is that numerous species and assemblages do not show marked environmental preferences. Studies of live diatom assemblages at single sites across the intertidal gradient can reveal close relationships to changes along a continuum of numerous ecological parameters that are also

associated with the intertidal elevation gradient (e.g. Nelson and Kashima, 1993). At a single specific site the sediment properties profile is more likely to show a gradient of decreasing particle size with elevation and the distribution of habitats with elevation is not blurred by the addition of data from different sites. Salinity can also show a more distinct continuum, often decreasing with elevation (e.g. Sherrod 1999), but the opposite can occur during the neap phase of the tidal cycle. Furthermore the live diatom assemblage does not suffer from the same degree of taphonomic overprinting that fossil assemblages do; the assemblage of interest in palaeoenvironmental investigations.

CHAPTER 6

PREDICTIVE MODEL DEVELOPMENT

6.1 Introduction

Chapter 5 examined the relationship between the diatom flora and environmental variables by means of descriptive analysis and TWINSPAN cluster analysis. This chapter goes on to quantify these relationships to determine statistically which environmental variables are most significant in explaining the variance in the diatom data, and what proportion of that variance these significant variables explain. The major environmental gradients in the data are then plotted on a CCA bi-plot to examine the species and samples associated with these significant variables. Individual species distributions along the normalised tidal height gradient are then examined to look for particular indicator species. Finally, a predictive model is developed using WA regression to model normalised tidal height values. A transfer function is also developed to predict habitat for each sample using analogue matching.

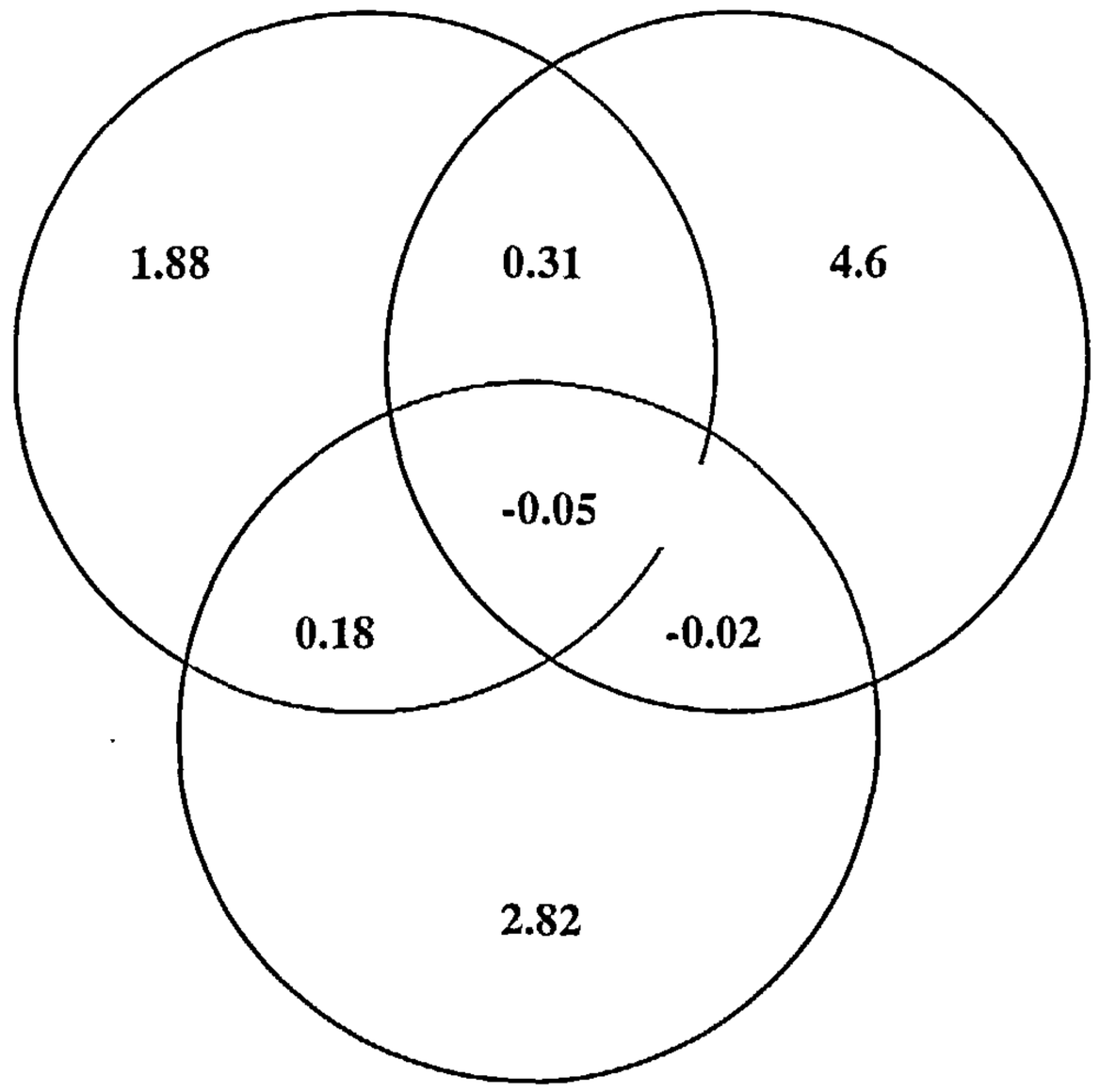
6.2 Diatom species distribution and environmental gradients

6.2.1 Variance partitioning

The methods used in this variance partitioning analysis are explained in section 4.6.3, along with the groupings of the environmental variables. Within the sediment properties group, percentage silt was found to be the most significant component and is therefore used to represent sediment properties. Silt is the dominant proportion of the majority of Samples so it is not surprising that changes in the proportion of silt is the most significant sediment property in terms of explaining variance within the diatom data.

The results of the variance partitioning exercise for normalised tidal height, salinity and sediment properties returns: (1) the variance explained by each variable in the total dataset with no other variables removed; (2) the unique variance explained by that variable (with the variance explained by the other variables already omitted); and (3) the total amount of

variance explained by all the variables together. These results can be used to calculate the variance explained by combinations of intersections of these variables. These results are shown in Figure 6.1.



Key

Number in outer circle	= unique variance explained by that variable (%)
Number in intersection of two circles only	= variance explained by intersection of those two variables only (%)
Number in intersection of al three circles	= variance explained by intersection of all three variables (%)

Figure 6.1 Percentage of the diatom data variance explained by combinations of different environmental variables. All explain variance with significance p >0.001, 999 permutations

6.2.1.1 Normalised tidal height, sediment properties and salinity

Together these three variables explain 0.528 of the total inertia value (a measure of the variance of the weighted averages within the diatom data) of 5.434. This is a total of 9.72 % of the variation. Sherrod (1999) carried out similar analysis on 22 diatom assemblages from

Lynch Cove in the Puget Sound, Washington and found salinity and elevation to explain 25.1% of the variance within the diatom data. This study had an almost linear salinity gradient across the intertidal habitat. This, coupled with the data having come from just one site as opposed to the 25 used in this study, is sufficient explanation for the increased significance of the salinity and elevation gradient in terms of explaining variation within the diatom data. Even in this study at one discrete site there are still clearly either other significant environmental variables exerting an ecological influence on the diatom distribution or a large impact due to taphonomic processes of redistribution (breakage was found to be minimal). In reality it is likely to be a combination of both.

Rather than focussing on results obtained from similar studies from individual sites, it is more relevant to compare Zong and Horton's (1999) result to the results of this study as they use a number of intertidal estuarine sites (six), also from Britain. Zong and Horton (1999) find that the percentage silt, clay, sand, LOI and elevation (normalised using their SWLI, see section 4.2.2) together account for 21.6% of the total explained variance. Some figures can be directly compared between Zong and Horton's (1999) study and this study. Sediment properties here account for 47% of the total explained variance using percentage silt as a proxy for sediment properties, whilst the silt fraction in Zong and Horton (1999) explains 5.2% of the total explained variance and sediment properties as a whole explain 35.2% of the total explained variance. It is particularly interesting that the most significant sediment property here is silt in terms of explaining diatom data variance, but in Zong and Horton (1999) it is LOI. Elevation, in the Zong and Horton (1999) study, explains a higher degree of the total explained variance (23.3%) compared to this study (19.3%). This suggests that the smaller training dataset has a stronger elevation signal compared to the larger one developed here, although both studies find sediment properties to be the most significant environmental variable in terms of explaining the variation within the diatom data. Zong and Horton (1999) include a larger number of samples from each individual site and this may also explain the higher significance in the diatom-elevation relationship as a more detailed intertidal profile is obtained from each site.

The large number of Sites in this dataset introduces a variety of correlations between the environmental variables measured. It has already been discussed that the sediment properties of an individual estuary are dependent on the provenance of that material and the hydrodynamic energy available to redistribute this material. Thus an elevation that in one estuary may be dominated by silts and clays, in another may be made up predominantly of

fine sand and silt. Conversely, although some estuaries do have larger proportions of sand content in the upper saltmarsh than the majority of estuaries, at this elevation many lower intertidal epipsammic forms would not be able to tolerate the degree of exposure. Salinity is also variable at similar elevations between Sites. Variations in all these three variables over such a large sampling area introduce a large degree of variation in the characteristic diatom assemblage associated with a given elevation, salinity class or grain-size profile.

Of the three major environmental gradients examined, sediment properties are the most important. As a unique variable, sediment properties uniquely explain 4.6 % of the variance, almost half of the total variance explained by all three variables together (see Figure 6.1). The variance explained by sediment properties for the whole dataset with no other variables removed only increases by 0.24% to 4.84% indicating that there is little interaction between sediment properties and the other two variables. One might expect a little interaction between elevation and sediment properties in terms of percentage sand as this does change by habitat type, and decreases fairly abruptly with increased elevation. As discussed in section 2.2.4, sediment properties of an estuary and its intertidal environment are also completely dependent on sediment supply and the energy of the tide and river flow, dictating the maximum size of sediment particle that can be entrained, carried in suspension and deposited. Whilst a strong relationship may be found between grain-size and tidal height within one particular estuary, the varied geological and hydrodynamic character of the estuaries within this dataset will diffuse any such relationship over the scale of this study area.

The variance explained by the intersection of normalised tidal height and salinity is also very low at 0.18% in Figure 6.1. Effectively showing no relationship between normalised tidal height and salinity in terms of acting together to produce similar changes in the diatom flora. Once again this is not unexpected as they are not naturally dependent variables. Whilst elevated salinities may be experienced on the upper saltmarsh during the neap tide cycle, the salinity level here can also be greatly reduced by precipitation. Furthermore, the average estuary water salinity at any one Site is dependent on its position within the estuary, (which determines the dilution factor between sea and fresh river water plus the type and depth of the salinity stratification (if any) at that point), and the phase of the tidal cycle.

As well as inter-site salinity variations, some transects show a large intra-site variation in pore-water salinity that does not follow a linear gradient (as found by Sherrod, 1999); such sites include Caerlaverock and Wigtown Bay (see Appendix 7). These two sites were

sampled during the neap phase of the tidal cycle and therefore the Sampling Sites had not experience tidal inundation for a number of days. This prolonged absence of the homogenising effect of tidal water on salinity across the transect would mean that pore-water salinity is left more vulnerable to atmospheric effects of dilution due to precipitation and concentration due to evaporation. Localised topography can also have a marked effect on water retention at any one point by either shading from evaporation, or increasing susceptibility to evaporation. Finally, localised freshwater incursion can have a strong impact on within-transect salinity variation in the absence of tidal waters and this is likely to explain the low salinities from the Sampling Sites at the back of Caerlaverock; the back saltmarsh (CK6) and high saltmarsh (CK5) Sampling Sites are both oligohaline, whilst the rest of the transect varies from meso- to polyhaline. Thus, intra-transect pore-water salinity can be highly variable.

In addition to the presence of widely varying salinities across some transects, other Sites may have a lack of salinity gradient due to the recent homogenising effects of tidal inundation, or precipitation. Furthermore, Sites that are sampled during the colder months of the year would be less affected by evaporation, and where there is no significant local source of freshwater this would further reduce intra-transect variability. Such sites include Alnmouth (see Appendix 7), sampled in December (1997), which exhibits a limited variation in salinity, from 12.2 g/l to 19.7 g/l, over an elevation gradient of 1 metre.

This lack of an apparent salinity gradient at a number of individual Sites, due to a variety of reasons, compounds the lack of relationship between salinity and normalised tidal height and adds further noise to the dataset.

Of all three variables, normalised tidal height explains the least amount of variance within the diatom data, 1.88% of the total variance. In other studies this gradient is found to explain a higher proportion of the total variance, such as 5.1% in Zong and Horton (1999). As already discussed, this lower level here is likely to be due to the larger variation in other measured and unmeasured environmental variables, and the greater heterogeneity of the diatom data in this large dataset. Despite this, normalised tidal height is still significant.

6.2.1.2 Habitat

After the variation within the diatom data set accounted for by salinity, normalised tidal height and sediment properties had been assessed, further partial CCAs were carried out to determine what quantity of the remaining variance is explained by the other variables of habitat and region. Habitat was tested next and only sandflat was found to be significant, accounting for a further 1.5% of the total variance in the dataset. That sandflat is the only significant habitat is to be expected from results of assemblage analysis in Chapter Five. Not only does the descriptive analysis of the flora from individual Sites in section 5.3 distinguish the sandflat habitat as having a particularly distinctive flora, but also the TWINSPAN analysis in section 5.4 discriminates Group Nine as having one of the strongest habitat affinities, consisting entirely of low elevation sandflat samples. The sediment properties of the majority of the rest of the habitats consisted of variations around the general description of predominance of silt with small proportions of sand and clay. Notwithstanding locally distinctive mudflat and saltmarsh assemblages, TWINSPAN analysis pointed to sand content as being one of the major factors defining the more distinctive groups (see table 5.5 and Figure 5.10). As sand content increases in this dataset, e.g. front of the marsh onto the muddy sandflat, so too does the distinctiveness of the diatom flora at a geographical level covering the whole study area. Percentage silt was found to be the most significant variable within the group of variables that make up the sediment properties. But in terms of habitat, high silt content can be found from the mudflats through to the high saltmarsh, so a high proportion of sand (almost exclusively only ever found on intertidal flats) is more important in terms of the ability of *habitats* to explain variance within the diatom data. The higher significance of the sandflat habitat compared to all the other habitats bears a direct relationship to the significance of the sand fraction within the sediment properties. As such, this habitat significance merely serves to strengthen the already identified significant of sediment properties in explaining the variance within the diatom data.

6.2.1.3 Regions

After the variance accounted for by the sandflat habitat classification, as a proxy for habitat, has been added to list of co-variables, regions are found to explain a further 14.1% of the remaining variance. This is a very significant result. Regions, or regionality, is found to explain half as much again as the amount of variance explained by sediment properties, salinity and normalised tidal height *together*. The regionality in the distribution of diatoms

began to emerge in the TWINSPAN analysis in section 5.4 but this exercise reveals just how significant this parameter is.

Local and regional variety in sediment provenance has already been discussed in section 6.2.1.1. This is likely to have a marked impact on the local and regional distribution of diatom flora. For example, the sediment provenance in the Solway Firth is predominantly sandy (Solway Firth Partnership, 1996) with high saltmarsh samples at both Caerlaverock and Bowness-on-Solway having a high proportion of sand content (CK5, 46% sand; BS1, 68% sand). In contrast, high saltmarsh sites throughout the Severn estuary consist predominantly of clay and silt (see Appendix 7) and, other than at Arlingham far upstream, there are no sandflat habitats at all. Thus this data set has a wide variety of sediment properties at similar elevations resulting in widely differing diatom assemblages and, conversely, different habitats at different elevations may share some key diatoms in common due to similarities in sediment properties. Areas of similar sediment provenance and hydrodynamic energy, such as the middle and lower Severn estuary, would therefore be likely, if taken in isolation, to produce a far less noisy dataset and hence a stronger diatom-elevation, diatom-sediment and diatom-habitat relationship. Other environmental variables that can exert an ecological pressure on diatom species and hence effect their distribution within the intertidal environment include pollution (organic, inorganic and directly toxic), local climate, turbidity increases, and impacts on the allochthonous component.

Nutrient levels within estuaries will vary naturally, but this natural variation is effected by human-induced eutrophication. Sources of additional nutrient supply to estuaries include sewage disposal, agricultural runoff and livestock grazing. Total levels of nutrients such as nitrogen and phosphate have been shown to have a marked influence on diatom assemblage composition in lakes (e.g. Allott and Flower, 1997; Bennion 1994; Hall and Smol, 1992) and rivers (Cox, 1991; Round, 1993; Schoeman 1972) and their impact on coastal diatom communities is also now being investigated in Denmark where coastal diatom assemblages are found to show a significant relationship to nutrient enrichment (Clarke, *pers. comm.*).

Fertilisation of agricultural land has been shown to be detectable in estuarine fossil diatom assemblages (Brush and Davis, 1984; Cooper, 1995) proving that agricultural activities can have an impact on the composition of estuarine diatom communities. This impact is not only in terms of increased nutrient supply, but also in terms of reduced dissolved oxygen content, a further parameter that effects diatom production and distribution (Darley, 1979). At a more

local level, livestock grazing on saltmarshes has been shown to have a marked effect on higher plant species diversity, sward height, sward density and soil properties (Ford and Grace, 1998). The additional nutrient supply will affect diatom assemblage composition and the shorter, denser vegetation sward will reduce light penetration to the sediment surface compared to a more open un-grazed saltmarsh sward. A number of sites within this dataset were being grazed at the time of sampling, such as Bowness-on-Solway and Wigtown Bay. Other sites, including Skyreburn Bay, Sailor's Holme and Hamford Water and Bridgewater Bay, showed evidence of grazing through one of more of the following: sediment poaching; stock fencing; livestock droppings; and closely cropped saltmarsh swards. In fact the majority of were either known to be grazed, or showed evidence of grazing with only a handful of sites free of any known grazing pressures; Blacktoft sands, Lymington and Poole Harbour being among the few.

Some sites British estuaries also receive a large amount of sewage waste, treated to different degrees, which has been shown to impact on the biology of the Firth of Forth (Waldron *et al.*, 2001). Not only does this elevate the nutrient content of the estuarine waters, along with sources of nutrients from agricultural runoff, but it enriches the saltmarsh where sewage-related debris can be deposited by the tides. Some sites exhibited clear signs of eutrophication, such as Sailor's Holme and Wentloodge, with thick algal growths in pools across the site, and other sites likely to be effected by eutrophication include those where sewage debris was seen such as the Exe. Since nutrients were not a parameter measured in this study it is not known what degree of nutrient elevation has been experienced at such sites nor is it possible to quantify this relationship in terms of driving the diatom assemblage composition. Zong and Horton (1998) recover a high percentage of eutrophic diatom species from a number of British saltmarsh environments, supporting the suggestion here that nutrient enrichment may exert a strong influence on the diatom flora in some estuaries despite the conclusion drawn by Denys (1991-1992) that the majority of estuarine and marine diatoms do not have a specific relationship with the nutrient gradient.

As discussed in Chapter Two (section 2.3), many British estuaries are the focus of high levels of industrial activity. Within this dataset the Humber would be a prime example. Shore-based industries discharge fluid wastes into the estuary, which may be augmented by industrial discharge further up in the river catchment, flowing down into the estuary. Diatoms are also sensitive to chemical pollutants such as heavy metals, sulphide and ammonia (studies on these subjects are summarised by Admiraal, 1984). As with elevated nutrient supplies,

these chemical pollutants not only alter the estuarine water chemistry, but they can also build up in saltmarsh deposits leading to high concentrations of pollutants such as the heavy metals cadmium, lead and zinc (Banus *et al.,* 1975) or radio-nuclides, as is the case in the saltmarsh of the Solway Firth (Johnson, 2001; Solway Firth Partnership, 1996). Silt particles can adsorb heavy metals, oil and other pollutants, which are then deposited with the silt grain in the intertidal habitat. The strong adsorption properties displayed by fine-grained sediment particles means that even naturally unpolluted sediments experience elevated levels of pollutants such as heavy metals (Admiraal, 1984). Barr *et al.* (1990) studied the infaunal community composition at 77 sampling stations throughout the whole of the Humber estuary and revealed that the changes in the biology of the sites correlated with levels of heavy metals, crude sewage and other industrial effluent, and that these levels varied considerably around the Humber, revealing that, even within an estuary the biology can change dramatically as a result of local pollution. The Wash is also affected, evident through the increased body load of mercury in winter wading birds (Parslow, 1975). The specific effect of toxic pollutants on a wide variety different estuarine diatom species is not known, but it is likely that these toxic effects will influence the diatoms directly and indirectly through impacts on diatom predators. Oil pollution is also a potential problem. Serious oil pollution incidences may result from large oil spill incidences, but, on a more continuous basis small amounts of oil are likely to be leaked into the estuarine environment from boat maintenance activities. Quite a number of Sites within the Study had oil films dotted around on the surface, more frequently at the back of the marsh (e.g. Sailors Holme, Stiffkey, Hamford Water and Wentloodge). Oil films can smother the surface preventing oxygen reaching the surface sediments. Areas affected by oil films were obviously avoided when selecting Sampling Points but the temporally homogenised subfossil samples may be affected by this phenomenon in regions with high levels of boats traffic, both recreational and economic, such as the South Coast, Southern East Anglia and the Humber. Pollution can also affect the ability of pioneer plant species to colonise an area (Baker, 1979), and hence the habitat and sediment properties may change.

The study area spans a latitudinal band of 5°. This is enough to introduce subtle differences in climate. The regions within the study area experience different daylight hour, temperature and rainfall regimes. The main effect daylight hours will have would be on the motile epipelon, which require different periods of light over the low-tide period to trigger migration to the surface to photosynthesise (Hopkins, 1966; Paterson, 1986). The rainfall regime has a strong impact on the average salinities on the upper saltmarsh and temperature. These

regional climatic changes may be very subtle in global terms, but for species existing at the limits of their tolerances for any of these variables small changes could be critical to their survival. What is also not known for this dataset is whether tidal magnitude and estuary type exert any influence on the diatom distribution.

This study takes the subfossil assemblage as a whole making no attempt to distinguish between autochthonous and allochthonous diatoms (see section 4.3.1). Over the scale of this study area it is possible, however, that changes that effect species making up part of the allochthonous component of the intertidal assemblage could introduce a further degree of unexplained variance. Some human activities will not have a direct impact on the autochthonous intertidal diatom flora in an estuary but they may exert a strong influence on the composition of the subtidal benthos and estuarine plankton. One example is shore-based power stations. Many power stations use coastal water as cooling water. This water is then discharged directly back into the estuary or coastal waters that it was pumped from. Although this does not introduce any significant chemical pollutants, the temperature of returned water is considerably elevated. This warming of the water alters the local flora and fauna and as temperature is known to effect diatom distribution it can be assumed to have an impact on the local plankton and subtidal benthos. Where a power station is situated such that currents move this water across Sampling Sites this will introduce a new component into the allochthonous flora. A second example is that of dredging. Estuaries with ports situated within them, such as the Humber, will undergo regular dredging to maintain a navigable channel for ships. Dredging greatly increases the turbidity of the water column and although this will not be a permanent effect, it is not known what influence this may have on the planktonic and subtidal diatoms, and hence the allochthonous component of the intertidal assemblages. Agricultural and silvicultural activities can also affect turbidity levels in the estuarine environment (Brush and Davis, 1984) and, in terms of this study, Dumfries and Galloway in particular has a large amount of land under forestry within its and this may effect sites such as Caerlaverock, Wigtown Bay and Skyreburn Bay.

Acidification of upland waters (streams and lakes) in Britain over recent decades is a well-documented phenomenon with its root cause in industrial emissions and local acid deposition exacerbated by climate patterns, poor buffering capacity of catchment geology and large-scale silviculture (see Mason, 1981; Smol *et al.*, Eds, 1986). Although the effects of upland regional acidification are likely to be significantly ameliorated by the time the acidified riverine waters reach the estuary, elevated levels may still be experienced. This is especially

likely in estuaries receiving water from rivers known to be strongly effected by acidification throughout their whole length, such as the Cree and Bladnoch that drain into Wigtown Bay (Solway Firth Partnership, 1996). Acidification alters the pH of the water, an environmental variables that has a significant impact on the floral composition of any diatom community (see section 2.6.2.2).

Altogether, then, there is a large suite of natural and human-induced ecological pressures that can vary from Site to Site, estuary to estuary and region to region. Some are subtler than others or more ephemeral in terms of their impact and contemporary pollution problems may be far lese serious than recent decades, but together they must expert powerful inter-regional and inter- and intra-estuary influences on the variation within the diatom data and thus result in a large degree of noise in the dataset. This has significant implications for the application of any transfer function developed from this dataset, to estuarine fossil diatom assemblages.

Horton (1997) analyses diatom assemblages from four intertidal sites on the North Sea coast. From the description of the dominant taxa given there appears to be quite a large degree of similarity between sites, which agrees with the results of the TWINSPAN analysis in Chapter Five where two Groups were shown to have a strong North Sea coast affinity. This suggests that a smaller scale study area might be more appropriate because, theoretically, the reduction in regional variation between North Sea sites would reduce the noise introduced by regional variation in this larger diatom dataset and hence allow a more accurate predictive model to be developed.

All these variables together (normalised tidal height, salinity, sediment properties, habitat and region) explain 25.3% of the variance within the dataset thus leaving a total of 74.7% unexplained variance. This indicates that not only is this a very noisy dataset but that there are likely to be other environmental variables, not tested here, that are also significant in explaining the diatom distribution. Zong and Horton (1999) find a similar total of 78% unexplained variance (but without habitat and regions tested) within the diatom data from six British intertidal sites and suggest that some of this unexplained variance may be due to between-site variation in diatom composition. The results of this study, with regions explaining the largest proportion of the explained variance, would support this suggestion. The noisy nature of estuarine diatom data is therefore clearly a key characteristic.

6.2.2 CCA results

Following the variance partitioning exercise CCA plots were developed for the significant environmental gradients, these being normalised tidal height, sediment properties, salinity, habitat and regions with additional environmental variance added as a passive variable. The DCA gradient length for normalised tidal height was found to be 0.38. Where a gradient measures less than 2 standard deviation units a unimodal rather than a linear response model is more appropriate for the training set (see Birks, 1995), thus justifying the use of CCA. The proportion of the variance explained has already been determined and we known the order of importance of the variables in terms of the degree of total diatom data variance they explain. The purpose of displaying the CCA bi-plots is therefore to look for Samples and Species that are correlated with particular environmental gradients.

6.2.2.1 CCA Axes one and two: sediment properties and salinity

Figure 6.2 shows the environment-samples bi-plot for the first and second axis. The arrows indicate the environmental variables; their orientation indicates the axis they are correlated with and their direction points towards increasing values. The length of the arrow relates to the strength of importance of the variable in terms of explaining the variance within the diatom data. Species and samples can be assessed according to their position relative to the gradient arrows with their position along the arrow reflecting their weighted average distribution. For presence/absence variables the centroids of the distribution are shown, rather than arrows, as a more meaningful reflecting of the nature of the data. This includes regions and habitats.

Sediment properties are correlated, as should be expected, with axis one, the most significant axis in terms of explaining the variance in the diatom data. Sand content plots in the opposite direction to percentage silt and clay. Salinity is associated with the second axis. Loss in ignition shows a correlation with the silt and clay gradient. This is likely to be a reflection of the fact that the higher vegetated habitats tend to have the higher silt and clay proportions and low amounts of sand. The higher vegetated environments accumulate more organic matter in the surface sediment through the presence of plant and tidal-rafted debris.

The species-environment bi-plot for axes one and two is shown beneath the sample-environment bi-plot in Figure 6.2. The environment arrows and centroids are omitted from

the printed species bi-plot in order to be able to distinguish the codes for individual species. Comparison of the species distributions with the environment arrows in the top sample-environment bi-plot indicates species that are correlated with particular gradients.

Species associated with sandy samples include *Amphora wiseii*, *Navicula arenaria*, *Fragilaria schulzii*, *Fallacia florinae*, *Fallacia cryptolyra*, and *Navicula finmarchica*. All these species have particularly low N_2 diversity values, all less than 4, and have only been recorded in abundances over 2% in sandflat samples, some at quite high abundances. Most of the *Fallacia* species encountered in this study are associated with the lower sandflat habitat suggesting a strong ecological as well as morphological affinity within the genus as a whole. *Amphora wiseii* is discussed further in section 6.3.4.

The salinity classes plot along the salinity gradient arrow revealing that salinity increases in a positive direction along axes two. Samples and species correlated with high salinity occur in the upper half of the bi-plot in Figure 6.2 and Samples and Species correlated with low salinities occur in the lower half of the bi-plot in Figure 6.2. A number of sites are correlated with the salinity gradient and the regions Southern East Anglia and the South Coast are aligned with this gradient at the higher salinity end. This suggests that salinity is a more important variable for the Sites in these regions than for other regions, and that salinity is more important in these regions than sediment properties in determining the diatom distribution. Also, these regions have, in general, higher salinity habitats within this dataset. Certainly, in the TWINSPAN analysis the southern mudflat and saltmarsh grouping, Group Three, is almost entirely made up of southern East Anglia and South Coast samples and this group also has the highest overall salinity class distribution (see section 5.4.3). In terms of habitats, dry pans are correlated with high salinities, as would be expected, with evaporation concentrating the tidal waters left behind in the pans. *Phragmites australis* (PH) is correlated with the lower end of the salinity gradient, confirming its status as an indicator of significant freshwater influence.

Species showing a strong correlation with the lowest salinities in the Figure 6.2 include *Navicula lucinensis, Achnanthes lanceolata, Nitzschia clausii, Denticula sundaysensis* and *Navicula cincta*. The first three in this list are quite rare in terms of the whole diatom data set and only found in the peaty back saltmarsh and *Phragmites australis* habitats, characteristically fresher habitats. Lower abundance species, in terms of this dataset, are likely to shower stronger correlations with environmental gradients because the smaller number of

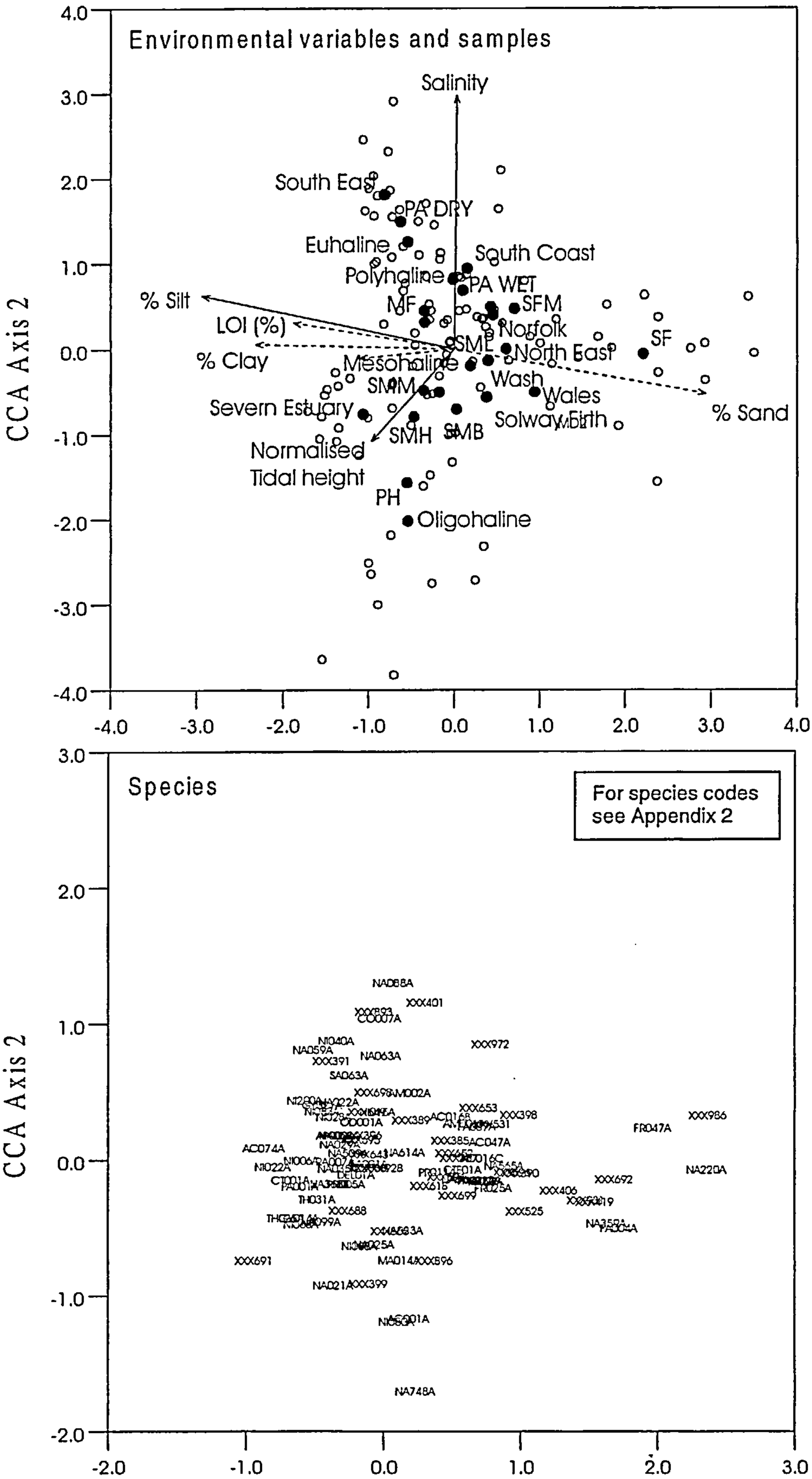


Figure 6.2 CCA bi-plot of axes one and two (o = Samples, • = environmental variables)

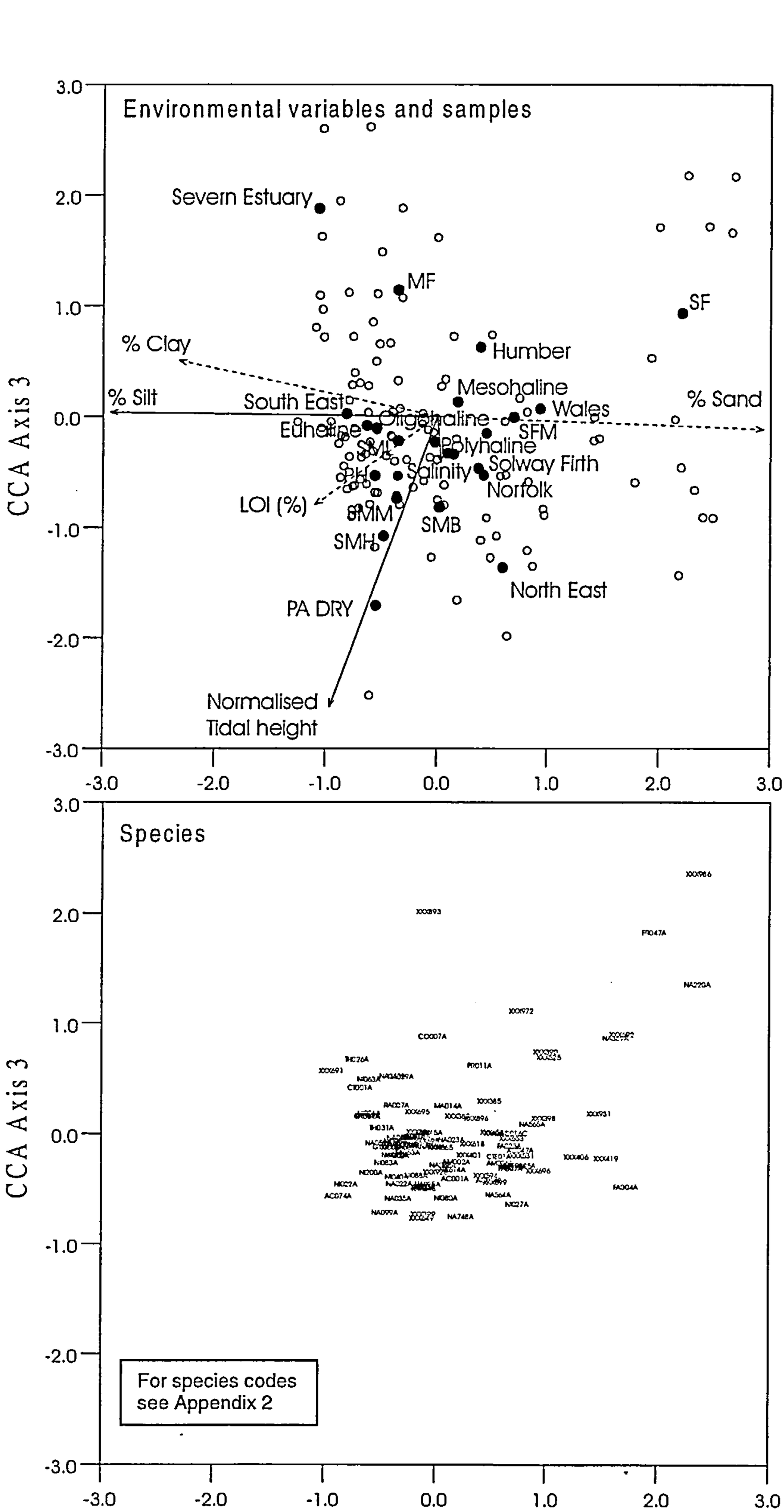


Figure 6.3 CCA bi-plot of axes one and three (o = Samples, • = environmental variables)

records reduces the noise in the relationship. The latter two species are more common, particularly *Navicula cincta,* and the TWINSPAN analysis has already identified these species as being characteristic of the higher elevation, often fresher, habitats. Species correlated with the highest salinities include *Navicula ryhncocephala*, *Navicula abscondita*, *Tabularia tabulata*, and *Cocconies scutellum.* All these are relatively low diversity species with an N_2 diversity less than 8, again maximising the signal to noise ratio in their distribution across environmental gradients. The distribution of *Navicula cincta* and *Cocconeis scutellum* over the intertidal gradient is discussed further in section 6.3.4.

The overall distribution of species over the CCA plot shows more of a distribution along the sand gradient and the full salinity gradient, with some species more closely correlated with the third axis, normalised tidal height (explored in section 6.2.2.2). The majority of species and Samples cluster towards the centre of the plot showing a strong correlation with the means of the environmental gradients. This reflects the problems encountered in the TWINSPAN analysis with the definition of any mid tidal range diatom groupings. The most distinctive groupings clustered around the extremes of the environmental gradients with a large number of species showing no particular affinity to any of the TWINSPAN groups delineated. Here in the CCA plot we see this tendency repeated, with only a small number of species displaying any strong correlation along particular environmental gradients. Estuarine diatoms do, however, have to cope with frequent changes in a number of different parameters, thus many species' distributions may not be strongly correlated with just one environmental variable as this may render them less adaptable to changes in conditions of another environmental variable.

Sherrod (1999) manages to encapsulate four habitat groupings within the distribution of the estuarine intertidal diatom species across a CCA species-environment bi-plot based on the first and second axes, represented by salinity and elevation respectively. The upper high marsh is a discrete group of diatoms correlated with the salinity gradient rather than the elevation gradient. The other three habitats identified by Sherrod (1999) from a CCA analysis include mudflat, low marsh and lower high marsh (roughly equivalent to the mid saltmarsh in this study) which are ordered along the elevation gradient with a small degree of overlap between habitats. Whilst species correlated with the extremes of the environmental gradients can be identified in this study, discrete habitat groupings such as those identified by Sherrod cannot be reliably delineated due to the concentration of species and samples around the centre of the plots and the generally noisy nature of the data.

6.2.2.2 CCA Axes two and three: sediment properties and normalised tidal height

The sample-environment bi-plot with axes one and three, sediment properties and normalised tidal height respectively, is shown in Figure 6.3. This plot of the first and third CCA axes shows a number of species that are correlated with the silt fraction, on the left hand side of the bi-plot, albeit towards the inner end of the gradient arrows. This correlation was harder to distinguish form the bi-plot of axes one and two in Figure 6.2. Species showing a correlation with fine and medium silt, and clay include *Gyrosigma litorale* and *Cymatosira belgica* and to a lesser extent *Rhaphoneis minutissima*, supporting earlier suggestions in Chapter Five that the latter two species, whilst having a wide-spread and frequently abundant distribution, are more strongly associated with the mid tidal range mudflat and low marsh habitats. Species showing a correlation with coarse silt include *Achnanthes groenlandica* and *Nitzschia fonticola*.

Some habitats, regions and Samples do appear to show a correlation with normalised tidal height. Samples and species in the upper half of the diagram correlate with low elevation and those in the lower right section of the bi-plot correlate with high elevations, although this relationship is not as strong as for axes one and two. Habitats correlated with higher elevation include dry pans, high, mid and back saltmarsh. These habitats are all more predictable in terms of their position along the tidal gradient compared to habitats such as mudflat, which can occur from below MLWS to around MHWN. Similarly, although it is unusual for pioneer marsh inception to begin below MHWN, depending on the stage of development of the estuary, this habitat can stretch quite far up the intertidal gradient whilst in other sites it may be absent altogether due to the presence of an erosional cliff between the high marsh and the intertidal flats. The mudflat and sandflat habitats plot out in the upper half of the bi-plot in Figure 6.3 showing a correlation with lower elevation. The centroid for the Humber region is aligned with the normalised tidal height gradient, but unlike most regions, it occurs at an elevation below ML. This reflects the higher number of low elevation Samples within the Humber region, such as the Spurn Point sandflat Samples, compared to the others.

Similarly to the plot of axes one and two in Figure 6.2, Figure 6.3 shows a clustering of habitat and region centroids around the upper mid tidal gradient, reflecting the predominance of Samples from this elevation.

Species distributions across axes one and three are shown in the lower of the two plots in Figure 6.3. Species correlated with the top of the intertidal gradient are *Navicula salinarum, Navicula bremensis, Denticula subtilis, Denticula sundaysensis* and *Navicula lucinensis*. In Figure 6.2 *Denticula sundaysensis* and *Navicula lucinensis* are also shown to be correlated with low salinity suggesting that they favour the high elevation fresh habitats, rather than the open high marsh susceptible to high salinities during the neap phase of the tidal cycle. At the other end of the tidal gradient, below ML, some species show a particularly close correlation, including *Palgiogramma brockmanii* and *Cocconeis neothumensis*. Continuing the tidal height arrow back to represent the tidal communities below ML places the arrow in the same quarter of the bi-plot as the percentage medium sand and percentage sand indicating a degree of correlation between these variables. What is particularly interesting is the group of species occurring more or less equidistant between the lower tidal gradient and the sand and medium sand gradients. Species include *Amphora wiseii, Fragilaria schulzii, Fallacia cassubiae, ,Navicula arenaira, Navicula finmarchica* and *Opephora marina* var. *minuta*. This indicates that these species are predominantly found on sandflat of low elevation as has been seen a number of time throughout the analysis; successive interpretive techniques strengthening earlier conclusions.

The distribution of species along the normalised tidal height gradient is explored further in section 6.3.

6.2.2.3 Partial CCA: regions and species

In order to explore further the regionality of the dataset, displayed in the geographical preference of a number of the TWINSPAN groups described in section 5.4 and discussed further in section 6.2.3.1, a partial CCA was carried out with all other environmental variables partialled out. The results are displayed on the regions-species bi-plot in Figure 6.4, in order to examine any regional groupings in the diatom species themselves and any associations between regions.

A number of relationships are immediately obvious in Figure 6.4. Apart from the one Site, Mawddach, which comprises the sum total of the region of Wales, there is a clear split in the plot between the more southern regions in the top half and the more northern regions in the bottom half suggesting a latitudinal/climatic element driving the dataset. Within this general pattern, a number of regions appear to show closer relationships than others. The Humber and

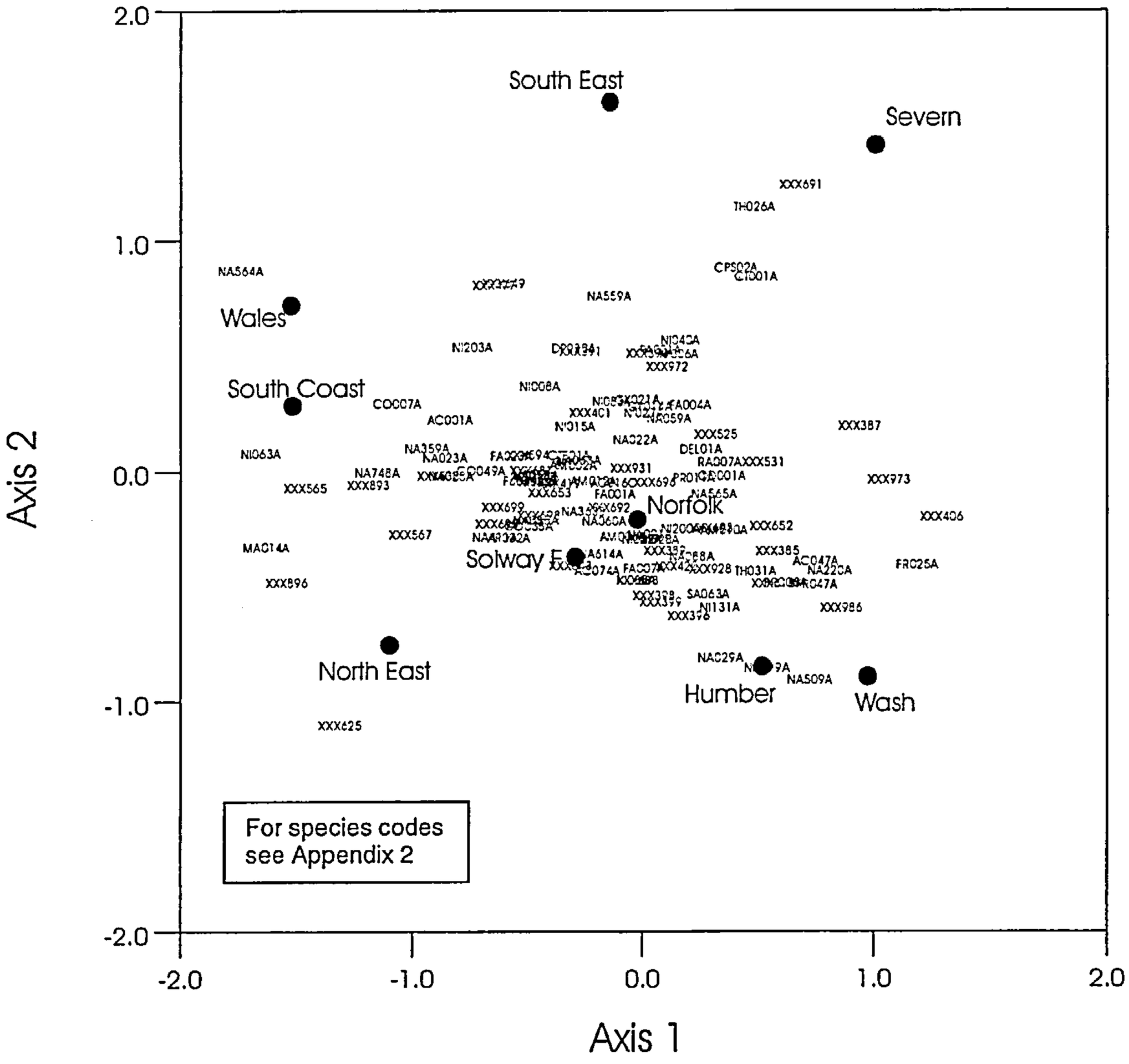


Figure 6.4 Partial CCA regions-species bi-plot (• = regions).

the Wash plot out close together in the bottom right-hand quartile of the plot. These two regions are closely situated along the eastern British coast and this result suggests a close association between the diatom floras from both regions. The regions of Norfolk and the North East are relatively near the Humber and the Wash suggesting a broad North Sea/east coast correlation in the diatom data. However, there are two factors that dilute this association, one being the proximity of the Solway Firth region in this area of the plot, and the other being the distance of the South East region – the other region from the east coast. It would appear that the South East region has a stronger association with the southern regions than it does with the east coast sites, possibly reflecting an interaction between the regions variable and sediment characteristics and habitat, or other factors discussed in section 6.2.1.3.

Wales has a closer correlation with the South Coast than any other region. This is an unexpected result due to the geographical distance between the regions. The Wales region is only made up of one Site; this association may, therefore, be somewhat artificial, potentially due to a number of key species also being found in abundance in one South Coast Site, or it is possible that there are a number of other unmeasured region characteristics, as discussed in section 6.2.1.3, coming in to play.

The TWINSPAN analysis in section 5.3 suggests two Groups (One and Two) with a strong Severn estuary bias and a third, Group Three, with a strong southern Britain bias (including the Severn). A number of species show a correlation with the Severn estuary in the top right-hand quartile of Figure 6.4; from strongest to weakest correlation these include *Gyrosigma litorale* (XXX691), *Thalassiosira oestrupii* (TH026A), *Campylosira cymbelliformis* (CPS02A) and *Cymatosira belgica* (CT001A). These four species are also those most closely correlated with the South East region. All these species also occur with greater frequency in TWINSPAN Groups One, Two and Three and thus the results of the cluster analysis are backed up the results of the qualitative analysis. However, what Figure 6.4 does not elucidate is the reason why these particular species show a preference, in his dataset, for the Severn estuary and southern Britain. A number of environmental characteristics of these southern Sites may be driving this preference. In the case of *Cymatosira belgica*, it has already been identified, in Chapter Five, as exhibiting a preference for silty habitats, prevalent in the Severn and South East, and there may be some interaction between the sediment and region variable here. Furthermore, Section 5.3.2.25 discusses the association between the presence of *Rhaphoneis minutissima* and *Cymatosira belgica* and notes that the latter species is less likely to be found along with the former in some of the more northern Sites, such as around the Solway Firth; a possible latitudinal preference is suggested. The results in Figure 6.4, together with analysis in Chapter 5, suggest that the key (measured) variables driving the geographical pattern in the distribution of *Cymatosira belgica* in this dataset are sediment properties and latitude/climate.

Navicula gracilis (NA029A), *Navicula bremensis* (NA099A) and *Navicula menaiana* (NA509A) all appear to show a correlation with the central North Sea regions of the Humber and the Wash. In the case of *Navicula gracilis* (NA029A) this does appear to be a relatively strong association. It is found in a total of 15 sites and 8 of these are from the Humber and the Wash, with a further 3 from Norfolk, and two from the North East, both regions that are near geographically, and also plot relatively near the Humber and Wash in Figure 6.4,

suggesting an east coast bias in the distribution of this species. *Navicula bremensis* (NA099A) and *Navicula menaiana* (NA509A), on the other hand, are found in as many Sites from without the Humber and the Wash as they are from within, the main difference being the higher abundance at which they are found in counts at one Site within either the Wash or the Humber. What, therefore, on the surface appears to be a strong regional correlation is in fact an artefact of a low abundance species, in term of the overall dataset, having its regional preference skewed by higher than average counts in Samples from one Site.

Wales, the South East and North East have a small number of individual species each showing a degree of correlation, but no distinct groups are seen and those species that do appear to show a correlation with any of these regions are all very rare within the dataset, and low in abundance when found. For example, *Gomphonemopsis exigua* var. *exigua* (XXX625) displays a close correlation with the North East in Figure 6.4. This is a rare species in this database, occurring in a total of 7 sites, always at low abundance. However, of these seven sites, three are at Alnmouth and the species occurs at slightly higher abundance in all three Alnmouth Sites than at any of the others outwith the regional, hence its regional association. *Rhopalodia constricta* (XXX896) shows a correlation with the North East as it is only found in one Sampling Site at Holy Island. As with the species associated with the Humber and Wash, the regional association of these species is more likely to be an artefact of a low abundance species, rather than a true regional association. However, further investigation of the regional flora and the distribution of rarer taxa with apparent regional associations in this dataset would be needed before firm conclusions can be drawn on this point.

The majority of diatom species plot out in the centre of Figure 6.4 suggesting no clear correlation with any one particular region confirming the cosmopolitan distribution of many diatom species, cited as a factor in favour of diatoms for this type of predictive model development in section 2.6.4. Apart from *Cymatosira belgica*, discussed above, all those species that show some correlation with individual regions, or groups of regions, are relatively low in abundance in the dataset. The regions of Norfolk and the Solway Firth are the most central in Figure 6.4, suggesting they have the least regionally distinct flora in the context of this dataset, Norfolk in particular.

Despite some regionality emerging in the distributions of some diatom species, in general the conclusion that can be drawn from Figure 6.4 is that there are few strong regional correlations in individual diatom species and even fewer in species that are abundant within the dataset.

Further Sites would need to be added to the dataset to draw firm conclusions on any geographical pattern to the distribution of less abundant species. It is therefore likely that the strong regionality exhibited in the diatom dataset is driven more by the composition of assemblages than individual species.

6.3 Diatom species distributions over the tidal gradient

The TWINSPAN and CCA analysis of the diatom data have shown tidal height to be a significant variable in terms of explaining variance within the dataset, thus justifying the development of a tidal-height transfer function. Before going on to develop the predictive model further this significant relationship between diatom assemblages and normalised tidal height and individual species can also be examined to further justify the development of the model. Significance testing of the distribution of diatom species along this gradient is performed, for 94 species with an abundance in any one sample greater that 5%. The method is discussed in section 4.6.4. The TWINSPAN and CCA results have focussed on diatom *assemblages*, but within these assemblages there will be individual *species* that are more or less indicative of different exposure times and hence elevation.

The significant model (null, linear, quadratic or GAM) for each species tested is given in Appendix 6. Of the 94 taxa tested, 68 fitted the GAM model, 2 fitted the quadratic model, 8 fitted the linear model and 16 fitted the null model. Thus 83% of the taxa tested have a significant distribution along the tidal gradient with the majority, 72%, fitting the most complex model. Species with particularly interesting distributions are discussed in the following sections and plots of within-sample abundance against normalised tidal range for these species are given in Figure 6.5. Optima and tolerance values for these species are shown in Table 6.1. Where species are suggested as being indicative of particular elevations, it should be remembered that this is indicative in terms of the fossil assemblage, not the living assemblage, where tolerances may be expected to be narrower.

Significance testing identified species with a significant distribution over the normalised tidal height gradient. This significant relationship is quantified by calculating weighted average optima and tolerances for species with an abundance greater than 2%. Figure 6.6 shows a plot of these optima and tolerances and supporting figure are shown in Appendix 6. Optima and tolerances for taxa shown in Figure 6.5 are included in Table 6.1. Weighted averaging is used

to produce the optima and this tends to truncate the data hence pulling in the more extreme values. This is particularly conspicuous in this dataset due to the large number of diatoms with optima between 0.5 and 1.0 normalised tidal heights, 64% of species tested. This is very evident in Figure 6.6. This means that the optima for higher and lower elevation species will be over and under estimated respectively and hence optima quoted may seem a little out of line with that indicated by the best-fit curves in the species distributions models shown in Figure 6.6. This overwhelming concentration of species around the upper central area of the tidal gradient in part reflects the predominance of Samples from this area of the tidal gradient thus elevating the proportion of upper-mid tidal gradient species in the dataset.

Examination of the table displaying species tolerances in Table 6.1 highlights the fact that the species with the broadest and the narrowest tolerances are some of the least abundant within the diatom dataset. These include, with broad tolerances, *Grammatophora oceanica, Nitzschia lorenziana, Navicula gracilis* and *Tabularia tabulata*, all with tolerances greater than 0.7 and N_2 diversity less than 5. Those with narrow tolerances include *Fragilaria capucina* var. *mesolepta, Gomphonemopsis exigua, Scoliopleura tumida, Nitzschia acuminata* var. *subconstricata,* and *Navicula lucinensis*, all with maximum abundances less than 5.5%, N_2 diversity less than 5 and normalised tidal gradient tolerances less than 0.2. Where a species has a low abundance and low diversity a realistic picture of their distribution may not be obtained because either an unusually high tolerance will be indicated (where a small number have been found in a small, but varied, number of Samples) or an unusually narrow tolerance is indicated (where a species has only been found in one or two Samples from very similar elevations). This finding emphasises the need to collect samples from a large number of sites in order to obtain a more realistic picture of the tolerance and optima of individual species along the tidal gradient.

Conversely, where species with very broad or particularly narrow tolerances also have high diversity and maximum abundance values it can be assumed that a more realistic impression of their distribution over the tidal gradient is obtained. An example would be *Navicula microdigitoradiata.* This species has a maximum abundance of 27% and a high N_2 diversity of 23 but it retains a narrow tidal gradient tolerance of 0.2, just one tenth of the breadth of the intertidal gradient. *Navicula microdigitoradiata's* high abundance value reveals that this species was found in a large number of Samples so its narrow tolerance is more reliable than those returned for species of low particularly low diversity.

Table 6.1 Distribution model fitted, optima and tolerance along the normalised tidal gradient, for species illustrated in Figure 6.6

Taxon Name	Model with best fit to tidal gradient data	Maximum percentage abundance	Number of samples containing taxon	N2 diversity	Optima	Tolerance
Achnanthes delicatula subsp. aff.*engelbrechtii*	GAM	18.9	9	3.93	0.68	0.35
Achnanthes delicatula subsp. *delicatula*	NS	10.3	49	18.27	0.61	0.34
Achnanthes delicatula subsp. *hauckiana*	GAM	21.1	100	33.23	0.47	0.44
Amphora wiseii	GAM	13.33	13	3.12	-0.61	0.62
Cocconeis neothumensis	L	5.5	24	9	-0.04	0.69
Cocconeis scutellum	GAM	28.5	53	8.08	0.13	0.72
Cymatosira belgica	GAM	30.5	77	34.11	0.53	0.41
Delphineis surirella	Q	7.3	74	33.78	0.62	0.33
Denticula subtilis	GAM	18.5	36	10.7	0.80	0.27
Denticula sundaysensis	GAM	19.0	15	3.67	0.97	0.12
Fallacia cassubiae	GAM	14.3	20	6.35	-0.20	0.67
Fallacia forcipata	Q	5.5	27	10.02	0.56	0.29
Fragilaria schulzii	GAM	10.8	18	3.93	-0.36	0.71
Gyrosigma peisonis	NS	8.2	66	30.43	0.61	0.36
Navicula c.f. *flagellifera*	GAM	18.5	64	17.56	0.55	0.29
Navicula cincta	GAM	61.2	76	18	0.82	0.28
Navicula flanatica	GAM	8.9	50	14.1	0.46	0.35
Navicula germanopolonica	GAM	24.8	71	17.35	0.31	0.54
Navicula gregaria	GAM	44.4	89	28.64	0.64	0.43
Navicula microdigitoradiata	GAM	26.8	61	23.1	0.70	0.23
Navicula mutica var. *mutica*	GAM	11.2	36	9.79	0.83	0.30
Navicula perminuta	GAM	34.0	105	39.05	0.42	0.52
Navicula phyllepta	GAM	30.8	88	33.69	0.59	0.31
Navicula sp. A	GAM	16.0	61	26.89	0.75	0.22
Nitzschia debilis	GAM	13.9	25	8.18	0.81	0.44
Paralia sulcata	NS	12.4	83	33.51	0.61	0.38
Rhaphoneis minutissima	GAM	44.0	112	63.97	0.52	0.39
Stauroneis salina	GAM	13.6	60	14.43	0.56	0.22

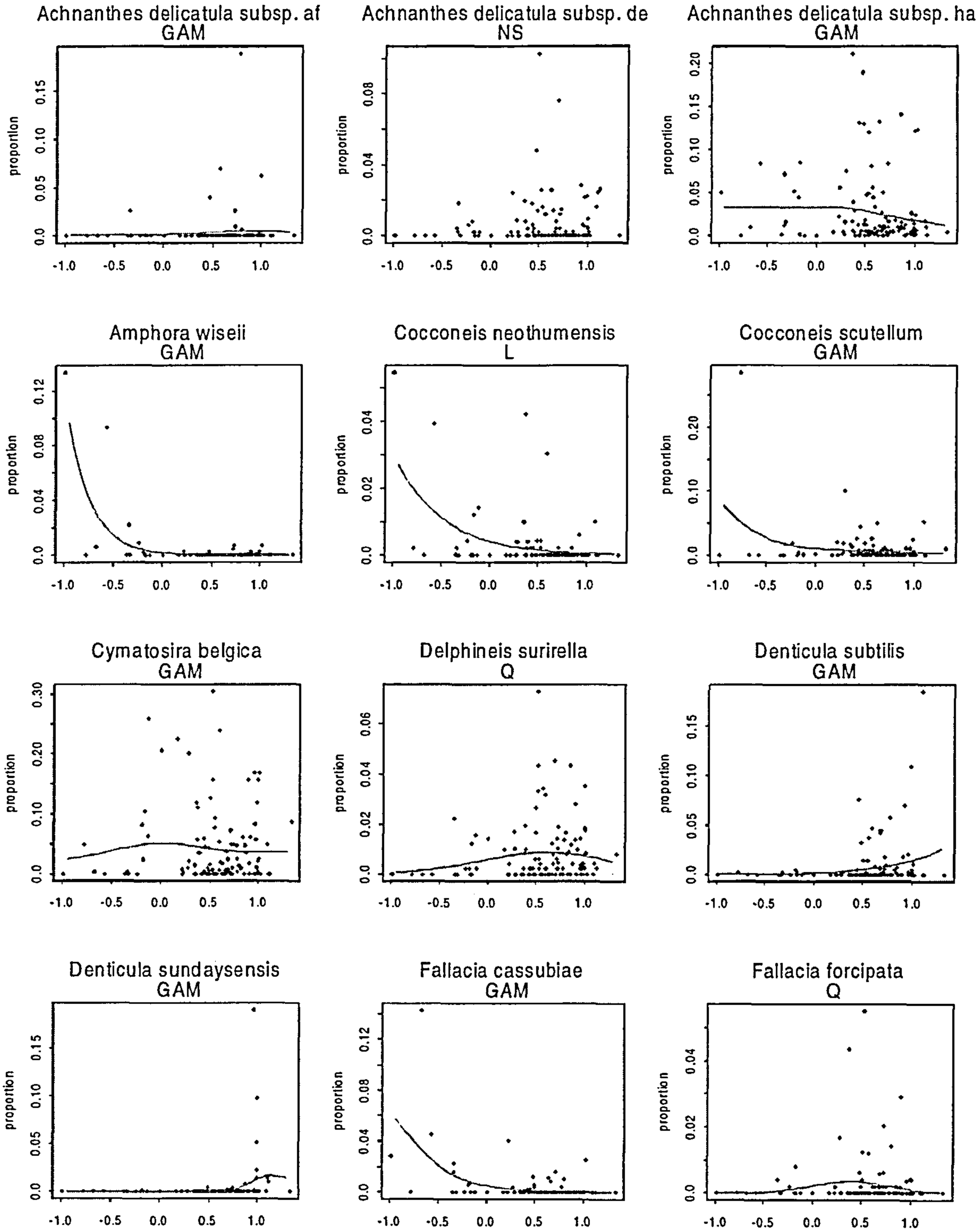


Figure 6.5 Plots of diatom species distributions over the normalised tidal height gradient, with the significant distribution model indicated

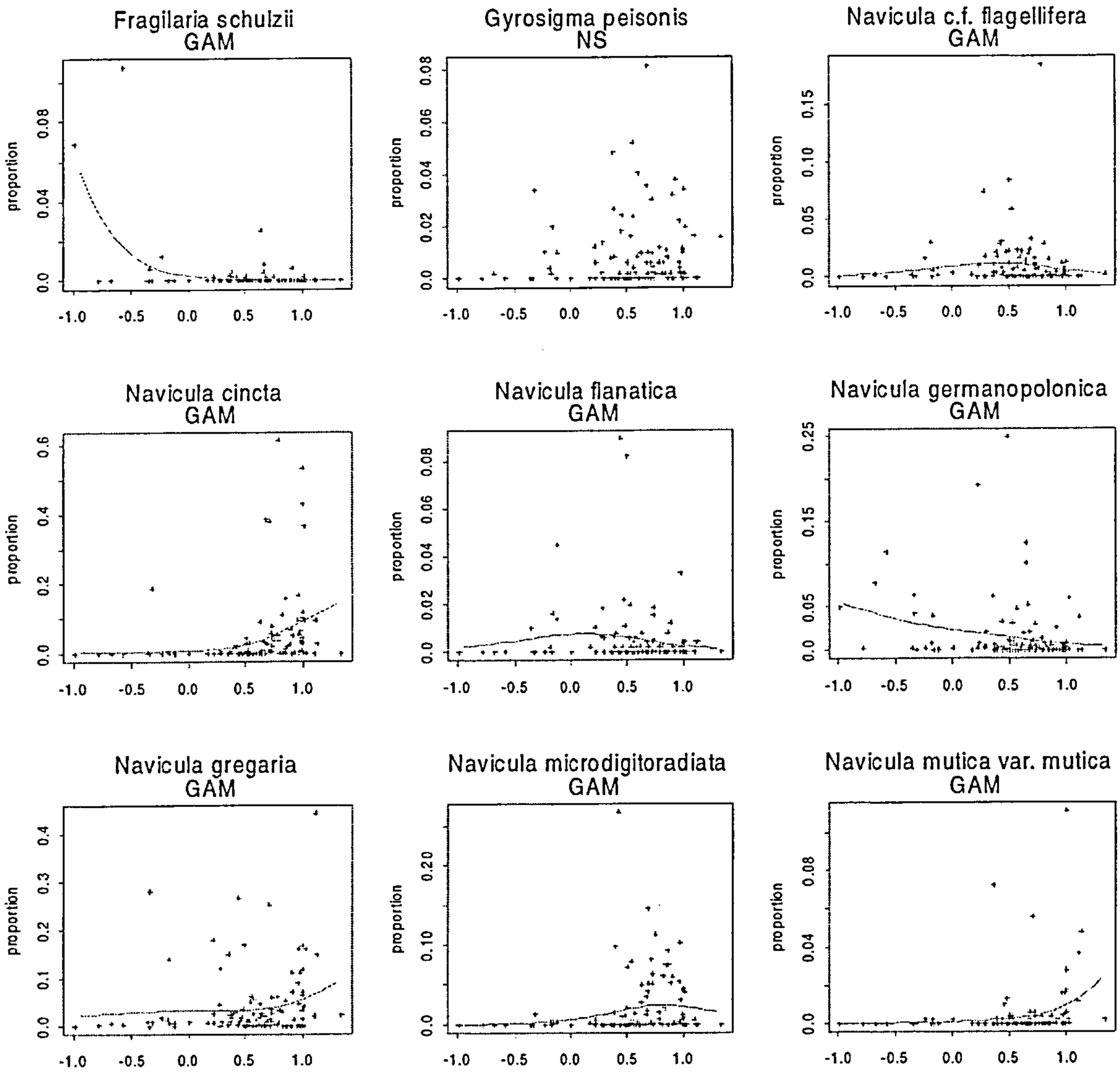


Figure 6.5 continued **Plots of diatom species distributions over the normalised tidal height gradient, with the significant distribution model indicated**

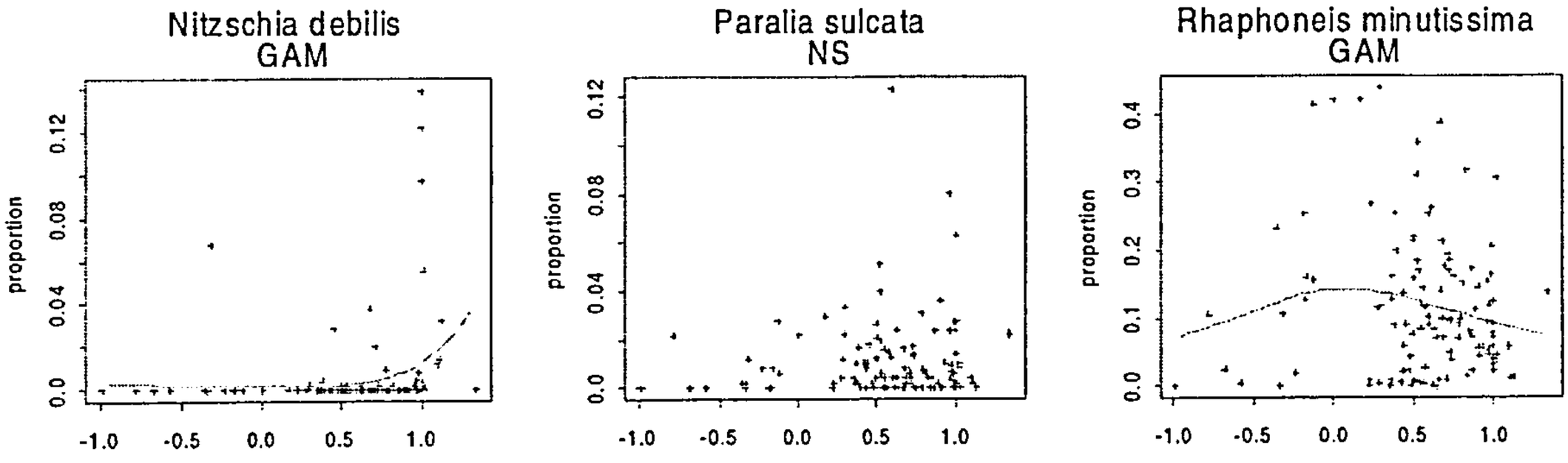


Figure 6.5 continued **Plots of diatom species distributions over the normalised tidal height gradient, with the significant distribution model indicated**

6.3.1 *Achnanthes delicatula* complex

Achnanthes delicatula subsp. *hauckiana* has already been identified as a fairly common species. The plot in Figure 6.6 shows a GAM fitted to the data, which is clearly rather noisy. Despite a number of samples with high abundances from above 0.5 on the normalised tidal height axis, the best-fit line for the GAM shows a continuous abundance from MLWS to just above ML then a steady decline towards the top of the tidal range. This pattern places *Achnanthes delicatula* subsp. *hauckiana* as a more important member of the mean to lower tidal range assemblages. Its optimum along the normalised tidal gradient is given as 0.47 (Table 6.1), somewhat higher than might be expected from examination of its distribution curve. This is mid-way between ML and MHWS. Intertidal flats are still common at this elevation, but it is likely that this figure is overestimated due to the large number of taxa with optima between 0.5 and 1.0.

The significance test for *Achnanthes delicatula* subsp. *hauckiana* adds weight to the suggestion made in Chapter Five that this species is more characteristic of the intertidal flats,

although it is frequently found on the saltmarsh at lower abundances. *Achnanthes delicatula* (with no distinction made between subspecies) is thought to be an epipsammic form living attached to sand and mud grains, susceptible to redistribution across into creeks and across the saltmarsh by tidal scour (De Jonge, 1985; Vos and De Wolf, 1993a), as are all species of this life-form. Sherrod (1999) finds *Achnanthes delicatula* subsp. *hauckiana* to be strongly associated with low elevations and the mudflat habitat and Horton (1997) finds *Achnanthes delicatula* to be dominant from low marsh and mudflat stations from Thornham marsh and Brancaster marsh on the North Norfolk Coast.

Of all the species in the *Achnanthes delicatula* complex this is the one with the most significant distribution along the tidal gradient. *Achnanthes delicatula* aff. *engelbrechtii* has a GAM distribution but it is of weak significance with only a very slight rise in abundance up the tidal gradient. *Achnanthes delicatula* subsp. *delicatula,* on the other and, does not have a significant distribution. This ecological difference in terms of distribution along the tidal gradient between sub-species within the *Achnanthes delicatula* complex supports the taxonomic identification to sub-species level as opposed to lumping all *delicatula*-type taxa together. Whilst the name *Achnanthes delicatula* subsp. *hauckiana* (Grunow and Lange-Bertalot 1991) is used in this study, this name is in fact a re-definition of an earlier name that places this taxon at species level; *Achnanthes hauckiana* (Grunow 1880). Its higher abundance and more significant tidal gradient distribution compared to the rest of the *delicatula* complex supports the separation of this taxon as an individual species on ecological grounds. More recently, the *Achnanthes delicatula* complex has been moved to a new genus, *Planothidium,* by Round and Buktiyarova (1996) with *Achnanthes delicatula* subsp. *hauckiana* being reinstated at species level, re-described as *Planothidium hauckianum* (Round and Buktiyarova, 1996).

6.3.2 Indicator species for the higher extreme of the tidal gradient

The most distinctive TWINSPAN Groups described in Chapter Five reflect habitats from the higher and lower ends of the tidal gradient. This pattern is picked up in the significance testing of species distributions along the tidal gradient, with the most distinctive distributions occurring for species skewed towards the high or low end of the tidal gradient. Species with a distribution skewed towards the upper end of the tidal gradient include *Denticula subtilis*, *Denticula sundaysensis*, *Navicula cincta*, *Navicula gregaria*, *Navicula mutica* and *Nitzschia debilis* (see Figure 6.5 and 6.4). Excepting *Navicula gregaria*, whose distributions spread a

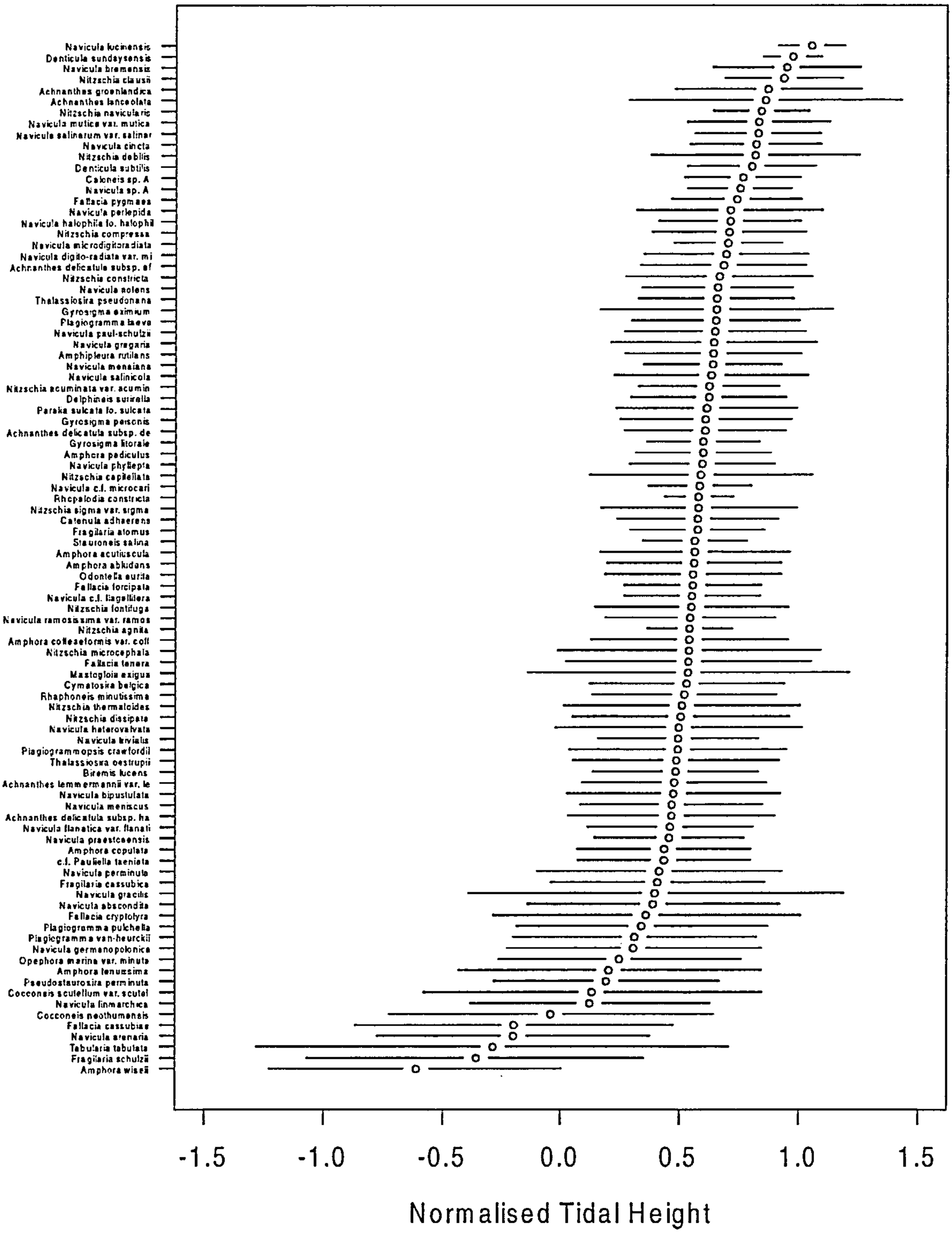


Figure 6.6 Optima and tolerances along the normalised tidal height gradient for selected taxa.

little lower down the tidal gradient, all these species have optima above 0.8, some of the highest optima returned (see Table 6.1). These species could be termed indicator species for habitats around MHWS. *Denticula sundaysensis* and *Navicula mutica* (as *Luticola mutica*) were also found to be indicative of high saltmarsh elevations by Sherrod (1999).

Denticula sundaysensis and *Denticula subtilis* are very similar morphologically, the key difference being an increase in striae density from *Denticula sundaysensis* to *Denticula subtilis*. This criterion was used to distinguish between the two species in this study but their close ecological preferences, especially in terms of distribution along the tidal gradient, suggest that perhaps these species are part of a continuum. Further study of these taxa would be needed to establish this, especially given the fairly recent arrival of *Denticula sundaysensis* as a record in coastal diatom studies and floras (despite its identification and description from the Great Sunday River of South Africa by Archibald in 1982). Of all the species identified as indicator species for the upper end of the tidal gradient, *Denticula subtilis* has the highest optima, at 0.97 and it is possible that this is slightly underestimated due to the predominance of species in the upper middle part of the tidal gradient optimum. *Denticula subtilis* is more likely to fall above MHWS judging by its distribution in this dataset.

Navicula cincta is described by Krammer and Lange-Bertalot (1986) as a fresh to brackish species and we have already seen this to be the case in this data set (see Figure 5.8). Its position as an indicator of the higher end of the tidal range may also be related to the occurrence of more freshwater habitats in this zone due to the increased important of freshwater runoff and precipitation over tidal waters. Hendy (1964) describe *Navicula cincta* as a supra-littoral species from the British coast. Other coastal diatom studies also define *Navicula cincta* as a typical saltmarsh and peaty back saltmarsh species (e.g. Campeau *et al.*, 1999). All these records are in keeping with the distribution found in this study. *Navicula cincta* is also aerophilic and motile (Campeau *et al.*, 1999). The former is a particularly crucial adaptation needed for any species to flourish in the high and back march environments, whose surface can dry out frequently and often for long stretches of time.

Navicula mutica is another aerophilous species, again supporting its definition here as a circa MHWS indicator species. Krammer and Lange-Bertalot (1986) cite *Navicula mutic*a as being common in fresh and brackish habitats. Although it is a prominent feature of the upper intertidal here, it is certainly not a particularly common species, an observation also made by Witkowski (1994) in his study of recent and fossil diatoms from the Gulf of Gdansk. In

contrast, Horton (1997) found *Navicula mutica* to be one of the most dominant diatoms from the high saltmarsh in Cowpen marsh within the Tees estuary, reaching a maximum abundance of 49%.

Krammer and Lange-Bertalot (1986) also describe *Nitzschia debilis* as an aerophilic diatom supporting its confined distribution within the upper most part of the intertidal gradient.

A species that has been hard to characterise in ecological terms throughout this study has been *Navicula gregaria*, with its widespread distribution (see Figure 6.6) blurring what appears to be an underlying preference for higher elevation, low salinity habitats. The significance test of its distribution over the tidal gradient is reassuring in its definition of this species as one that is significantly more indicative of the top of the tidal range than any other area, with a visible increase in the fitted response curve around MHWS. Its optimum, in Table 6.1, is given as 0.64, below MHWS but falls in the upper quarter of the tidal range. Its tolerance is given as 0.43, broader than the other higher elevation indicator species, but still within 25% of the intertidal gradient. However, caution should be urged in placing too much faith in a high abundance of *Navicula gregaria* as being indicative of a tidal level around MHWS due to the generally noisy nature of its tidal range distribution.

In Figure 6.6 *Navicula* sp. A shows a clear affinity for the higher elevations with a normalised tidal range value between 0.5 and 1.0, having an optimum of 0.75 and a narrow tolerance of 0.22. This problematic taxon would be worthy of further investigation using electron microscopy to inspect the finer morphological features and hence assist in identification as it clearly has potential as an indicator of a tidal range between 0.5 and 1.0 along the normalised tidal gradient.

In addition to taxa with a strong association with the upper extreme of the tidal gradient there are some species that have significant distribution around a normalised tidal level value of 0.5. This is midway between ML and MHWS but cannot be assumed to be indicative of an elevation associated with MHWN as this tidal level does not necessarily fall equidistant between ML and MHWS. Species whose distribution indicates an affinity with this level include *Delphineis surirella*, *Fallacia forcipata*, c.f. *Navicula flagellifera*, *Navicula microdigitoradiata* and *Stauroneis salina* (see Figure 6.6). None of the best-fit curves for the models fitted to this group of species show a particularly strong peak around normalised tide level 0.5, but there is clearly an association with this elevation. *Delphineis surirella* and

Fallacia forcipata are the only two diatoms with a quadratic model fitted, hence exhibiting a classic Gaussian distribution along the intertidal gradient with an optima around 0.5. Given the rather broad distributions of these species their use as indicator species should be employed with caution with peak abundances taken as indicative of a normalised tidal level around 0.5 but not as firm confirmation. *Delphineis surirella* and *Fallacia forcipata* are likely to be more reliable than the other species quoted.

6.3.3 Mean level indicator species

This is a more difficult region of the normalised tidal range for which to pin down indicator species. Although species with an optimum closest to zero should be ideal, there are few species with a clearly defined peak at this point. Even in a study of estuarine intertidal diatom distribution at one site Sherrod (1999) found no clear species pattern within the low and mid saltmarsh. Nevertheless there are some species that do appear to be broadly indicative of ML, although all have very noisy distributions in general. These species, whose tidal gradient distribution plots are shown in Figure 6.6, include *Cymatosira belgica*, *Navicula flanatica*, *and Rhaphoneis minutissima*. The widespread distribution of these taxa throughout most of the tidal gradient suggests that these species should only be taken as indicative of ML in large datasets where the majority of higher abundance samples can be distinguished from samples with moderate abundances. Given the interpretive problems *Rhaphoneis minutissima*, and to a lesser extent *Cymatosira belgica*, have caused throughout this study it is reassuring to see that *Rhaphoneis minutissima* in particular does appear to show some tidal gradient pattern with a greater affinity for habitats around ML. The optimum for *Rhaphoneis minutissima* is given as 0.52 and for *Cymatosira belgica*, 0.53. Given that these are likely to be slightly overestimated, for reasons already discussed, this shows a good match between the modelled distributions and the qualitative conclusions drawn on these species distributions in Chapter Five. This tidal gradient distribution, together with the correlation of *Rhaphoneis minutissima* and *Cymatosira belgica* with the silt and clay gradient in the CCA plot in Figure 6.3, clarifies the optimum estuarine environmental conditions for these taxa. With a good understanding of the modern distributions of these species there is no reason why they should not be employed in estuarine palaeoenvironmental and palaeotidal reconstructions as long as their indicative results are interpreted in a broad rather then narrow manor.

Navicula phyllepta, another particularly common estuarine species both in the literature and in this study, also has a fairly noisy but significant distribution across the tidal gradient. From

the graph in Figure 6.5 it appears to be more indicative of habitats just below, to a little above, a normalised tidal height value of 0.5 supported by its optimum value of 0.59 and tolerance of 0.31. It is not, however, a particularly strong peak. TWINSPAN analysis suggested that this species was associated with silty habitats around and above ML. It could be that the tidal distribution shown in Figure 6.5 and 6.4 is in part an artefact of the lack of many particularly low tidal mudflat samples, where, potentially *Navicula phyllepta* might also be relatively abundant. However, Witkowski (1994) records it as a species found in sandy habitats, whereas Witkowski *et al.* (2000) simply state that is tolerant of a wide variety of salinities. Given the varied and conflicting information available on this species, its indicative value in term of the tidal gradient should not be relied upon.

6.3.4 Indicator species for the lower extreme of the tidal gradient

As mentioned in the section 6.3.2, the lower extreme of the intertidal gradient, similarly to the upper extreme, has a number of taxa with closely associated distributions. All the species modelled as having a significant skew towards increased abundance below ML have already been identified as characteristic of sandflat habitats (TWINSPAN Group Nine) or intertidal flats and mudflat habitats (TWINSPAN groups Eight and Two respectively). These species include *Amphora wiseii, Cocconeis neothumensis, Cocconeis scutellum, Fallacia cassubiae, Fragilaria schulzii, Navicula germanopolonica* and *Navicula perminuta* (see Figure 6.6). Optima (Table 6.1) for these species range from –0.61 (*Amphora wiseii*) to 0.42 (*Navicula perminuta*). The habitats below ML are the significantly under-represented in the dataset compared to those above and species whose optima fall in this lower half of the tidal gradient are therefore likely to suffer the most from truncation of the data range in the calculation of weighted average optima. These optima can all be assumed to fall lower than the given value. All these species have broad tolerance values in Table 6.1 ranging from 0.5 to 0.72. This reflects their wide distribution up into higher elevation habitats through taphonomic processes of redistribution.

These lower elevation species suffer more redistribution around intertidal environments than any other groups. There are a number of likely reasons for this. Firstly, coming from a habitat that is either always or very frequently immersed in·water with a lower salinity fluctuation than higher up the gradient could make it an easier habitat to adapt to and to flourish in in high abundances. Secondly, unattached epipsammic forms are highly vulnerable to tidal redistribution due to the mobile and un-cohesive nature of the sandflats and

the free movement of interstitial water. Thirdly, low elevation taxa inhabit an area more frequently (or permanently, in the case of epiphytic *Cocconeis* species) inundated by the tide potentially leading to higher numbers in suspension in the tidal waters than species from higher-elevation habitats.

De Jonge (1985) in a study of epipsammic diatom populations found that sand grains in the water had a similar number of diatoms attached per grain to those on the intertidal flat, which indicates a large flux of epipsammic forms into the creeks and marsh. 80% of diatoms present in sandy sediments (particle size > 55 μm) were found in or attached to the mud coating on the sand grains highlighting the importance of the presence of certain levels of finer grained material. De Jonge suggests that this latter finding renders the terms 'epipelic' and 'epipsammic' unhelpful in terms of life-form classification. The frequent high abundance of apparently 'epipsammic' forms, such as *Navicula perminuta*, on mudflats and apparently 'epipelic' forms on the sandflats, e.g. *Achnanthes delicatula* subsp. *hauckiana*, may well be explained by this phenomemon.

Amphora wiseii has the lowest optimum at –0.61 and can be seen to be distinctly separate at the tail end of the plot of species optima in Figure 6.6. This a small but distinctive species encountered in 13 Samples and exhibiting a clear tidal gradient preference. *Amphora wiseii* also features on the CCA species environment bi-plot in Figure 6.2 as the species that correlates with the coarsest particle size refining its value as an indicator to species to one of low elevation sandflats with very little silt of clay content. Witkowski (1994) records it as a marine polyhaline species and although absent from the recent flora of the Gulf of Gdansk, it was found as a rare but constant component of the fossil flora. It has also been found as a common member of the recent flora from the Danish coastal water (Clarke, *pers. comm.*). Pankow (1976) also records *Amphora wiseii* as a marine polyhaline species. Form this study it would appear that it is either an epipsammic form, or an epiphytic form living on plants from the subtidal environment (see the discussion of *Cocconeis* species below).

The two *Cocconeis* species have different fitted models (Table 6.1, Figure 6.5). *Cocconeis neothumensis* shows a linear relationship to the tidal gradient and *Cocconeis scutellum* having a more complex GAM model fitted. The idealised distribution of an individual species over an environmental gradient are assumed to follow a unimodal curve showing a peak in abundance around an optimum condition, with an exponential decline in species abundance above and below the optimum. Where a linear model is fitted to a species distribution along

an environmental gradient it is possible that only one 'tail' of the hypothetical unimodal distribution curve is being picked up in the dataset. This may well be the case for *Cocconeis neothumensis* whose peak abundance in terms of elevation probably falls below lowest low water. Campeau *et al.* (1999) record *Cocconeis neothumensis* as an epiphyte. As there is no vegetation on the sandflats that *Cocconeis neothumensis* is commonly found in in this study, it is likely that it is living attached to plants, including macroalgae, from the lowest tidal extreme and subtidal habitats of these sites. They are probably being brought up on to the lower sandflats by the tide and therefore its linear distribution model may well be representing the upper tail of a unimodal species distribution curve.

Cocconeis scutellum is also an epiphyte described by Witkowski *et al.* (2000) as a cosmopolitan epiphyte in brackish and marine waters. Horton (1997) finds it in abundance in the low elevation habitats from Thornham and Brancaster marshes, North Norfolk, and Welwick marsh in the Humber. Its common high abundance on the lower sandflats in this study is probably the result of a mechanism similar to that proposed for *Cocconeis neothumensis*. The CCA bi-plot in Figure 6.2 shows *Cocconeis scutellum* to be strongly correlated with a high salinity, polyhaline and euhaline environment. This, together with the tidal gradient distribution points to a species most commonly found on the low intertidal sandflats in the outer reaches of estuaries, where the salinity is higher. Seaweeds can be found in saltmarsh habitats either attached to the woody stems of plants such as *Halimione portulacoides*, or freely on the sediment surface (see Chapman, 1976). *Cocconeis* species associated with these macroalgae may well, therefore, be found in significant number in some samples from higher up the tidal gradient. This phenomenon, along with post-mortem tidal transportation may account for the scatter of moderate abundances of *Cocconeis neothumensis* and *Cocconeis scutellum* within habitats above ML.

Species showing a linear model, or monotonic GAM distribution, cannot be assumed to follow a Gaussian distribution outside the intertidal range as the environmental variable that is being modelled here does not continue into the sub- and supratidal zones. But where appropriate ecological information is available about a species, the linear model can be taken as indicating a peak in abundance outwith the intertidal gradient.

Witkowski (1994) found *Fallacia cassubiae* to be an abundant species in the coastal shallows of the Gulf of Gdansk which is in keeping with its definition here as an extreme low intertidal elevation species. *Fragilaria schulzii* is described by Witkowski *et al.* (2000) as being

widespread from the sandy marine littoral and sublittoral of the northern hemisphere, also supporting its position here as a species strongly indicative of an elevation around and probably below MLWS.

Navicula germanopolonica is a relatively newly-identified taxa described by Witkowski and Lange Bertalot in 1993 (in Lange-Bertalot, 1993). But since its publication it has been identified in a number of coastal diatom studies and floras (e.g. Campeau *et al.*, 1999; Clarke, pers. comm.; Snoeijs and Potapova, 1995; Witkowski, 1994) showing it to be a common coastal diatom and indicative of the need for the publication of more large-scale coastal and marine diatom taxonomic work. Witkowski (1994) finds *Navicula germanopolonica* to be one of the most common species from the recent and subfossil flora of the Gulf of Gdansk, reaching its highest abundance in sandy sediments to a water depth of 5m. In this study it does not have as strong a skew towards the lower extreme of the tidal range as some other species, due to a large number of moderately high abundance records above ML (see Figure 6.5). This is also reflected in its rather higher than expected (despite over-estimation) optima of 0.31. This distribution above ML, especially into silty habitats, can be assumed to be due to taphonomic processes with *Navicula germanopolonica* remaining a good indicator of the lower portion of the intertidal and, judging by Witkowski's (1994) results, of elevations below MLWS as well.

The last species identified as indicative of the lower half of the tidal range is *Navicula perminuta*. This has already been seen to be a species with a wide distribution throughout the dataset but reached its highest consistent abundances in TWINSPAN groups Eight and Nine, intertidal flats and sandflat groups respectively. From the model of its distribution along the tidal gradient, in Figure 6.5, it is clear that it has a noisy distribution that increases in significance gradually down the tidal range exhibiting a steeper rise in abundance below ML. Its optimum is the highest of any of the lower elevation species, at 0.42. Krammer and Lange-Bertalot (1986) describe *Navicula perminuta* as being cosmopolitan in river mouths and marine coasts, a distribution evidently reflected in this dataset. It is also recorded as an epipsammic form by Campeau *et al.* (1999), again supported in this study, and a clear indication of why it is appearing as a low elevation diatom. It is not as good an indicator of the extreme low end of the tidal range as the species already discussed above, but it is, nonetheless, an important component of the diatom flora from below ML. Witkowski (1994) identifies a species that is morphologically very similar to *Navicula perminuta* but he retains it as c.f. *Navicula perminuta* due to minor unresolvable differences. If similar forms to

Navicula perminuta occur commonly in coastal and marine habitats, but with different ecological preferences, then it is possible that without the aid of electron microscopy some of these morphologically close species have been misidentified here as *Navicula perminuta*, adding to the noisy spread of this species over the tidal gradient.

6.3.5 Diatoms with no significant relationship to the tidal gradient

As mentioned at the beginning of section 6.3, 16 of the 94 species analysed did not have a significant distribution over the normalised tidal height gradient. The generally noisy nature of the diatom dataset renders this result unsurprising.

In the descriptive and TWINSPAN analyses in Chapter Five some *Gyrosigma* species appeared to show an affinity with the higher intertidal habitats, a pattern also picked up by Sherrod (1999) in Puget Sound. But *Gyrosigma peisonis*, one of the more common and abundant *Gyrosigma* species (N_2 30.4), does not show a significant distribution across the tidal gradient in Figure 6.5, suggesting that other environmental parameters are also exerting an influence in defining its ecological distribution. Van de Werff and Hulls (1976) describe *Gyrosigma peisonis* as a fresh to brackish species so it may be that salinity rather than elevation is a more critical environmental variable for this species. Tidal redistribution could also help explain this non significant distribution.

It is interesting to note that a number of the species without significant distributions along the tidal gradient include a number of the commonly found estuarine planktonic species. Amongst these is *Paralia sulcata*, whose plot is shown in Figure 6.5. Such robust centric forms, whilst forming a familiar component of any intertidal samples in almost any coastal diatom study, bear no relationship to the tidal gradient. So, as long as there are sufficient numbers of other taxa within any given sample or dataset, the presence of these species should not interfere with quantitative reconstructions of estuarine environmental variables.

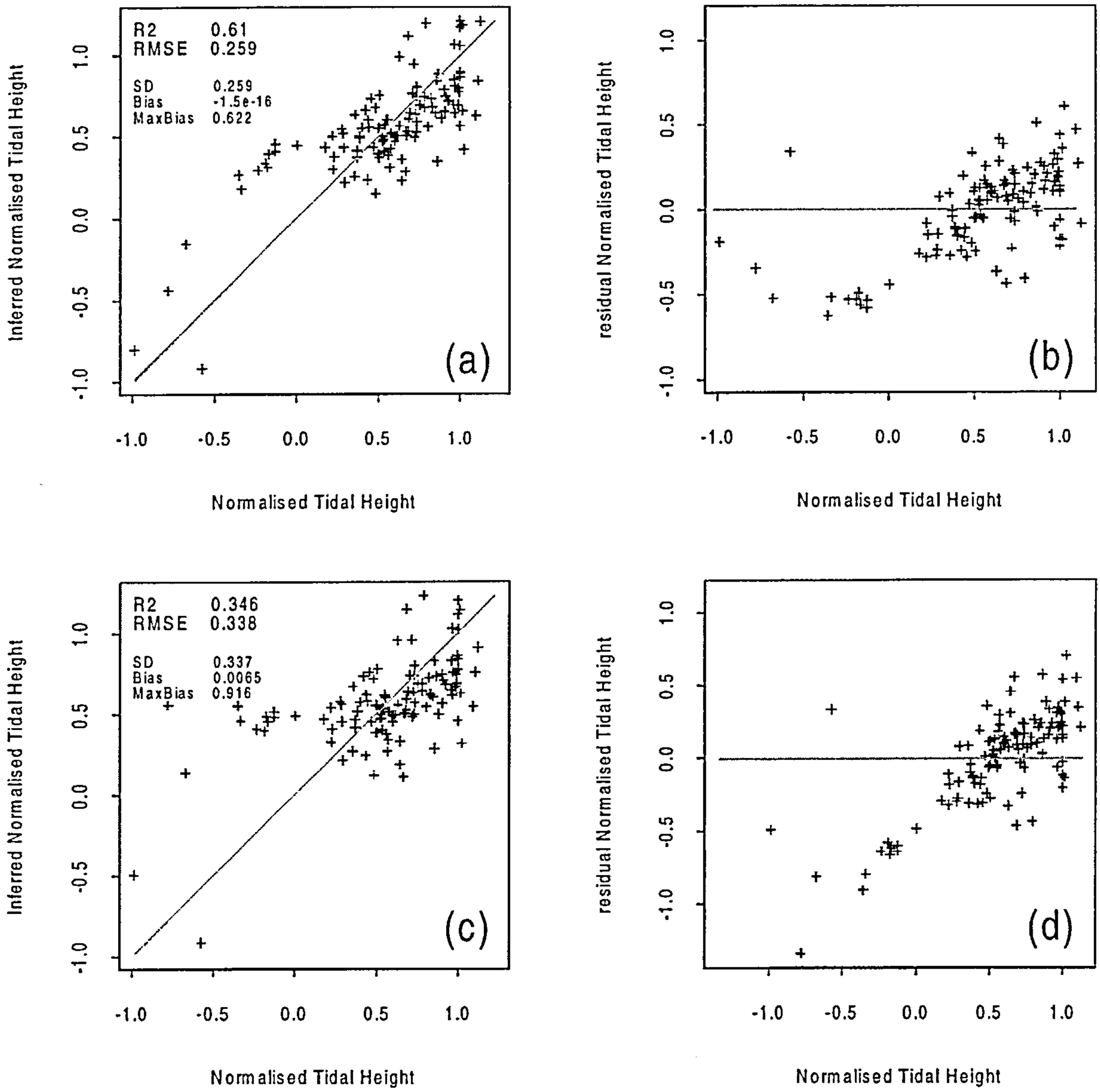
Of the 16 taxa with no significant distribution over the intertidal gradient nearly all of them have either particularly high N_2 diversity values (greater than 20) or low N_2 diversity values (less than 10). A number of the high diversity species have just been explained as being estuarine planktonic forms. A number of the low diversity species with no significant relationship are also estuarine planktonic forms such as *Thalassiosira pseudonana*. For other estuarine low diversity species returning no significant distribution along the intertidal

gradient, this is likely to be because there were not enough records of the taxa for a significant tidal gradient relationship to being to emerge.

6.4 Diatom-based tidal calibration model

CCA forward selection has shown that normalised tidal height is a significant variable in explaining variance within the diatom data, justifying the development of a predictive model for this variable. The method for developing the WA regression transfer function for normalised tidal height is explained in section 4.6.5. Three outliers, DB4, SM5 and SP3, were identified as having standard residual measurement greater than 2.5 and were therefore removed from the model. The results of the weighted average calibration model for apparent and jack-knifed predictions (see section 4.6.5) are shown in Figure 6.7 along with a plot of the associated residuals. Estimation errors for the two models are given on the graphs. Other methods of prediction were also tested including WA-PLS, but this was not found to improve on the WA regression model. Tidal height values for absolute, relative to ML and normalised tidal height are given Appendix 7.

Both the apparent and jack-knifed models in Figure 6.7 clearly show the predominance of samples from above ML. As a consequence the samples below ML are all, with one exception, overestimated in the model, their estimated elevation being pulled up by the effect of the large number of upper mid tidal range samples on the weighted averages. This highlights a practical problem in terms of data collection. The lower half of the intertidal gradient in an estuary consists of intertidal flat habitats. Where the intertidal flats are predominantly sandy, such as at Spurn Point, access to the lower shore is easy and safe. Where the intertidal flats are muddy access to the lower shore becomes very difficult, time consuming and often unsafe because of the difficultly in traversing the soft muds. In many estuaries it is simply impossible due to the depth of the soft mud. Furthermore, the lowest elevation habitats on very broad intertidal environments are often beyond the range of the surveying equipment. Although the station can be set up lower down the intertidal gradient, moving the station introduces additional errors and it is not always practically possible to transport the equipment down to a suitable elevation. In some instances, the intertidal environment is so broad that, although sediments might be firm enough to reach the lowest tide level, the time taken to reach the site on foot and to sample it leads to the risk of being cut



KEY: (a), Apparent normalised tidal height predictions; (b) Apparent normalised tidal height predictions residuals; (c) Jack-knifed normalised tidal height predictions; (d) Jack-knifed normalised tidal height predictions residuals

Figure 6.7 Weighted average calibration model for apparent and jack-knifed predictions

off by incoming tides (as is the case in the inner Solway Firth). These practical and safety obstacles explain the bias in the samples towards Samples above ML.

The apparent inferred values are more accurate than those predicted by jack-knifing as would be expected. A higher r^2 shows a better predictive ability and a higher RMSE shows greater errors of prediction and the RMSE and r^2 values for the apparent predicted values are 0.259 and 0.61 respectively whilst the $RMSE_{jack}$ and r^2 for the jack-knifed model are 0.338 and

0.35. The jack-knifed model is a more realistic picture of the accuracy of the model in predicting tidal height because it bases the predicted value of a Sample on the dataset with that sample, which is the way in which the model would be used to reconstruct tidal height from core material.

The jack-knifed predictions in Figure 6.7 show a considerable scatter around the one to one line of the model. This has a higher error of prediction than found in similar studies for a single, or a smaller number, of sites. For example, Sherrod (1999) develops a diatom-based transfer function to predict elevation and salinity from the Puget Sound, Washington. The r^2 value retuned for the elevation reconstruction was 0.72, whilst the r^2 for this model is 0.61. Sherrod also found that the predictive ability of the transfer function was greater for the mid elevation samples that for those falling at the extremes of the elevation gradient. This is similar to this model with the zone around and above MWHN returning the closest predictions. Figure 6.7 displays a large number of Samples between 0.5 and 1.0 normalised tidal height being predicted with far greater accuracy than the higher and lower elevation samples, many of these upper mid elevation Samples falling within a normalised tidal range of 0.25 to either side of the one to one line. Zong and Horton (1999) find the strongest vertical zonation gradient in the diatom from six British estuarine sites to be from around MHWN to above HAT, which also agrees with the findings here.

The implications of the model developed here for palaeoenvironmental reconstructions in the estuarine environment are discussed in section 6.6.

6.4.1 Effect of embankments

The possible effects of the presence of artificial structures interrupting the tidal gradient, such as seas walls and embankment, are discussed in section 3.2. Figure 6.8 classifies the Sites in the diatom-based tidal calibration model according to those that are embanked (including sea walls) and those that are not. It is clear from Figure 6.8 that there is no strong trend in the embanked sites in terms of ability to predict. There is a suggestion that embanked Sites are slightly less likely to have the tidal height predicted as lower than the true height, due to the wider scatter of Sampling Sites from embanked Sites below the line, but there is no pattern for Sites that have been over-predicted. However, a t-test was performed to establish whether the mean of the residuals was significantly different between the embanked and non-embanked sites, i.e. whether the residuals of embanked or non-embanked sites have a

tendency to over or under predict. The t-test was not significant. Therefore, the presence of embankments has no significant effect on the performance of this model.

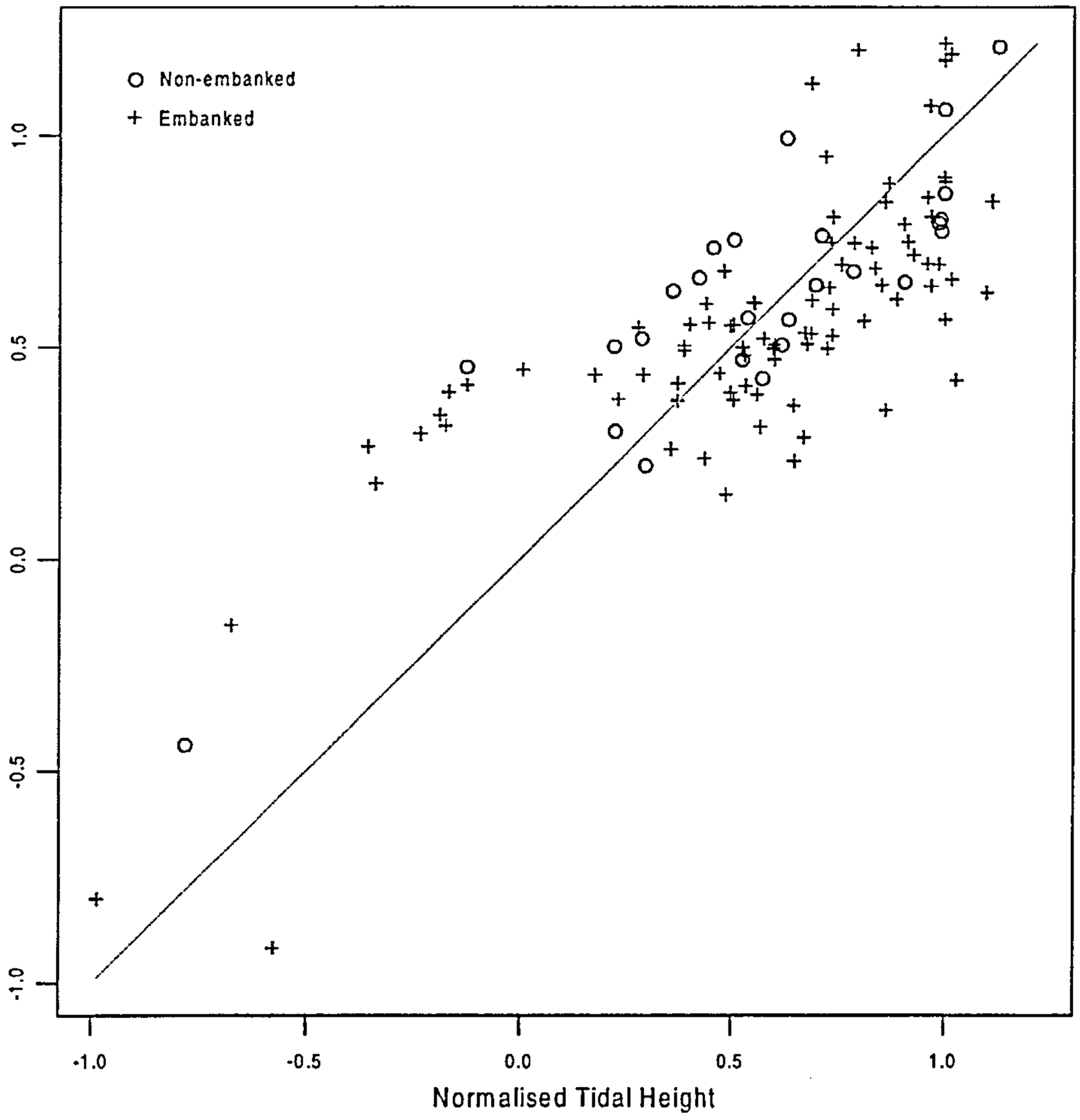


Figure 6.8 Weighted average calibration model for jack-knifed predictions identifying Sites with and without embankments or sea walls.

6.4.2 Regional diatom-based tidal calibration model

The large number of sites in this study clearly introduces a considerable amount of noise into the model. Greater proportions of the variance within the diatom data have already been seen to be explained by regions, sediment properties and salinity. At one local site or a number of sites within one estuary, the diatom flora may show a strong relationship to the tidal gradient. However, over larger geographical areas a wide variety of estuaries are introduced in terms of hydrodynamics, sediment provenance, microclimate, and human impacts (such as pollution,

Table 6.2 Regional diatom-based calibration models

Region or Group of regions	Range of normalised tidal height	Number of Samples	Number of species	WA apparent predictions errors			WA jack-knifed predictions errors		
				r^2	RMSE	Max. bias	r^2	RMSE	Max. bias
Global model (see Figure 6.7)	-0.99 – 1.12	113		0.61	0.259	0.62	0.35	0.34	0.91
Humber	-0.99 – 1.0	16	145	0.91	0.16	0.28	0.76	0.25	0.15
Norfolk	-0.68 – 0.91	9	139	0.84	0.20	0.28	0.01	0.61	1.18
North East	0.22 – 1.0	12	148	0.83	0.10	-0.09	0.14	0.22	0.40
Severn	-0.12 – 1.0	14	119	0.76	0.18	0.34	0.61	0.23	0.46
Solway	-0.36 – 1.13	18	150	0.82	0.15	0.42	0.40	0.27	0.97
South Coast	-0.78 – 0.99	11	140	0.93	0.12	0.25	0.09	0.44	1.13
South East	-0.17 – 1.1	11	127	0.89	0.12	-0.19	0.66	0.22	0.39
Wales	-0.34 – 1.03	5	116	0.91	0.16	-0.27	0.39	0.75	-1.16
Wash	0.39 – 1.01	17	147	0.75	0.10	-0.15	0.16	0.18	0.27
East coast/North Sea regions (Humber, Norfolk, North East, South East, Wash)	-0.99 – 1.10	65	178	0.69	0.22	0.62	0.50	0.28	0.70
West coast regions (Solway, Wales, Severn)	-0.36 – 1.12	37	164	0.71	0.22	0.41	0.22	0.37	0.98
Southern regions (South Coast, Severn South East)	-0.78 – 1.10	36	166	0.73	0.22	0.38	0.25	0.36	1.25
Northern regions (Solway, Norfolk, North East, Humber, Wash)	-0.99 – 1.12	72	181	0.72	0.21	0.67	0.55	0.26	0.99
Wales + South Coast	-0.78 – 1.02	16	157	0.87	0.17	0.23	0.02	0.49	1.13
Severn + South Coast	-0.78 – 1.02	25	159	0.77	0.21	0.39	0.23	0.39	1.19
Severn + South East	-0.17 – 1.10	25	152	0.74	0.19	0.27	0.46	0.28	0.46

grazing and sea wall construction). These other variables, over such a large area exert a more significant effect on the diatom flora than the constant variable of the normalised intertidal gradient. The variance partitioning exercise in section 6.2.1 reveals regions to be the variable

that explained the largest amount of variance within the diatom data and the likely causes of this are discussed in section 6.2.1.3.

In order to explore further the importance of regions within the dataset a series of regional diatom-based calibration models were generated and the results are shown in Table 6.2. Without exception, all permutations of regional apparent models perform better than the global model, but it is the jack-knifed models that are the best grounds for comparison in terms of the true performance of the models. On the basis of the r^2 value, seven regional models have a higher predictive ability than the global model, retuning values higher than 0.346, these include: the Humber; the Severn; The Solway; the South East; the East Coast; the Northern Regions; and the Severn and South East. Of these regions the Humber has the highest r^2 at 0.76, followed by the South East and the Severn. The Humber also has a large number of samples and one of the largest normalised tidal height ranges, making a fuller dataset than many of the other individual regions. In terms of predictive ability then, individual regions perform the best, and in fact the Severn and the Humber are actually individual estuaries, suggesting the predictive ability of a diatom-based tidal calibration model will be improved by focussing on a single estuary. Yet the Wash and Wales, both also individual estuarine systems, whilst having a lower RMSE than the global model, do not show any greater predictive ability in terms of the r^2 value, engendering caution in making any assumption that individual estuaries will consistently generate better models. In addition, the utility of such models based on single estuarine systems is questionable, in terms of palaeoenvironmental reconstructions, given the limited number of modern habitats covered and hence the increasing likelihood of no-analogue situations, for both diatom species and environmental variables, when applied to samples from palaeoenvironments.

Of the amalgamated regional groupings only the East Coast and the Northern Regions groupings perform better than the global model, (but not as well as the Humber, Severn or South East). Both of these regional groupings are suggested by the TWINSPAN analysis (see Table 5.7) and, to a degree, by the partial CCA of regions and species in Figure 6.4. The Severn and South East model also performs better than the global model with a slightly higher r^2 and slightly lower RMSE. This regional grouping also shows up clearly in the regions-species bi-plot in Figure 6.4, strengthening the suggestion that there are a number of affinities between these regions.

In many cases the ability of the models to predict does decrease when moving from individual regions, to amalgamated regions, to the global model. This is contrary to the experience in palaeolimnology where the merging of increasing numbers of samples from an increasing number of sites does not adversely effect the signal-to-noise ratio of the dataset, but does improve the resultant predictive model by adding greater detail in terms of diatom species and the environmental variables measured, hence reducing no-analogue situations when applying the model to palaeoenvironmental reconstructions. An example is the successful diatom-based phosphorous transfer function developed by Bennion (1994) with samples from 123 lowland British lakes. When compared to the lake environment, the coastal environment is far more dynamic with a larger number of environmental gradients impacting on diatom distributions and these environmental gradients can have different relationships to each other, and to the key variable of tidal height, at different sites. Hence, merging data from different coastal sites, whilst decreasing the number of likely no analogue situations, increases the noise in a dataset in a manner not encountered with lakes.

Despite a number of individual regions and regional grouping models performing better than the global model, there are just as many that do not perform as well as the global model, these include: Norfolk; the North East; the South Coast; the Wash; West Coast; Southern Regions; Wales and South Coast; and Severn and South Coast. These results are interesting as the TWINSPAN analysis in Chapter 5 suggests that some of the Groups have a southern character, but the Southern Regions grouping and Severn and South Coast do not perform well as calibration models. It is likely, therefore, that the southern character of some of the Groups in the TWINSPAN analysis are driven more by the Severn and South East, which do perform together better than the global mode, than any factors relating to the South Coast region. It is perhaps not surprising that the Norfolk model does not perform well as, in Figure 6.4, it appears in the middle of the bi-plot where the majority of diatom species occurred, suggesting a lack of a distinctive flora, which would effect the model's ability to predict from a diatom dataset generated solely from within that region. The Norfolk region also has a small number of sites (9) reducing the number of analogues in the dataset. The poor performance of the North East model, which has a large number of species in comparison to other individual regions, may be in part due to the limited normalised tidal height range within the regional dataset.

The Wales and South Coast grouping was tested because of the proximity of these regions on the region-species bi-plot in Figure 6.4, but the poor performance of this particular model

confirms earlier suggestions that there is no specific affinity between these sites, a few similar species possibly driving the proximity of these regions on the bi-plot in Figure 6.4. Although similarities between sites is not the key to generating a successful model, indeed it is diversity that is needed to reduce no-analogue situations, sites that are potentially different in terms of sediment-elevation relationships and the distribution of other environmental variables with elevation, as with the South Coast and Mawddach (Wales), can only adversely affect the signal-to-noise ratio of a dataset and the predictive ability it terms of evaluation in the resultant model.

In general it can be seen that there are as many regional models performing worse than the global transfer function as there are performing better. This has significant implications for the type of sites that are chosen for the purposes of amalgamation to create a regional diatom-based predictive model for elevation (normalised tidal height). It also has implications for the current debate on local versus national datasets for developing predictive models (see section 26.7). Whilst some regions generate a more accurate model, the heterogeneity of some regions/regional groupings actually generates a poorer model than a larger global transfer function; this needs to be the focus of further study.

6.5 Habitat Transfer Function

A transfer function is developed for predicting habitat from the diatom data. This is done using a simple analogue matching technique to predict habitats. The method is described in section 4.6.5. The analogue matching technique that predicts the highest number of habitats correctly is the square chord coefficient. The model uses all 466 taxa identified. Predictions were also carried only including species over 2% abundance and species over 5% abundance, but in this instance the full training set performed most successfully.

In the presentation of the results in Table 6.3 some habitats are merged based on ecological similarities because the subtly of the numerous habitat variation over the intertidal gradient could not be expected to be picked up in fossil material. High, mid and back saltmarsh are merged with dry pans and are represented simply as saltmarsh. Creeks, mudflats and sandy mudflats are merged and represented as the intertidal flats (as reflected in TWINSPAN Group Eight, section 5.4.8). Wet pans are merged with intertidal flats as they share the majority of their ecological characteristics with this habitat grouping. Sandflat is kept separate, despite it

also qualifying under the broad title of intertidal flats, because of the distinctive flora associated with this habitat as revealed at all stages of the data analysis. Pioneer saltmarsh is also maintained as a separate habitat, being a transitional community between the saltmarsh and intertidal flats. Finally, *Phragmites australis* is also retained as a habitat category because it is a distinct habitat in its own right.

The results of the habitat predictions are given in Table 6.3. The shaded cells in the table represents those count of habitats that are predicted correctly. From this table it can be seen that 66 of the 116 samples are predicted correctly, a success rate of 59%.

Table 6.3 Habitat predictions from the diatom data using analogue matching

Predicted habitat ↓	**Actual habitat**				
	Sandflat	Intertidal flats	Low/pioneer saltmarsh	Saltmarsh	Phragmites australis
Sandflat	9	11	0	1	0
Intertidal flats	4	30	9	6	2
Low/pioneer saltmarsh	0	5	7	5	0
Saltmarsh	0	5	3	19	2
Phragmites australis	0	0	0	2	1

Phragmites australis is the habitat that is predicted with the least accuracy from this dataset. Only one of five samples is predicted correctly although two more are predicted as the neighbouring saltmarsh community. Analysis of the average abundance of species within habitats in section 5.3.3 showed that the *Phragmites australis* and high saltmarsh habitats share a large number of common taxa so this result is not surprising. The final two *Phragmites australis* Samples are predicted as mudflat. Although these are very different environments in terms of elevation and salinity (mudflats having a broad range of classes and *Phragmites australis* being oligohaline) they can share a number of other ecological characteristics, most notably surface sediment properties. Furthermore, in this dataset two of

the Sites were *Phragmites australis* habitats were sampled did not have a transitional saltmarsh between the mudflats and the Phragmites beds, the latter abutting directly on to the former (these are Blacktoft Sands in the Humber and Poole Harbour).

The saltmarsh habitat grouping is predicted with 58% success rate with 19 of the 33 saltmarsh Samples being retuned in as the correct habitat type (Table 6.3). This habitat shows the greatest spread in predicted habitats across the tidal range with six being predicted as intertidal flats and one as a sandflat. Descriptive analysis of individual sites in section 5.3.2, TWINSPAN analysis in section 5.4 and significance testing of the distribution of individual species along the tidal gradient all reveal the high degree to which many species autochthonous to the intertidal flats can be distributed by the tide onto the saltmarsh, where the reduced energy of the tidal flood waters often favours deposition of fine particles.

Within the saltmarsh grouping, the high saltmarsh is the habitat with the highest degree of accuracy in prediction. This reflects the more distinctive flora associated with this habitat, seen in the TWINSPAN analysis in Chapter Five and the species distribution models across the normalised tidal height gradient (see section 6.3.4). Sherrod (1999) finds the upper saltmarsh to be the most distinctive and discrete habitat assemblage and Zong and Horton (1999) find this elevation zone to have the most distinctive diatom vertical zonation suggesting that this is a widespread phenomenon. The relationship between elevation and exposure (the ecological variable for which elevation is acting as a proxy) has been shown by Gehrels (2000) to change into the high saltmarsh elevation (see section 4.4.2) with small increases in elevation leading to large decreases in flooding frequency. It is possible that this marked change in the flooding frequency gradient breaking up the continuum across the elevation gradient not only produces a more distinctive autochthonous flora in the high saltmarsh, but also reduces the degree to which lower elevation and subtidal species are deposited in this habitat, although spring tides may deposit large amounts of allochthonous valves over one or two tides leading to the sub-fossil assemblage occasionally resembling the intertidal flats.

In terms of the diatom flora in the low saltmarsh Samples, Table 6.3 shows more habitats being predicted as intertidal flat than low marsh, with 3 predicted to fall within the general saltmarsh habitat type. The low marsh occurs around and just above MHWN (see section 2.2.5). This tidal threshold marks a crucial difference in the number of inundations an environment experiences over a season or a year. The fact that far more low saltmarsh

samples are predicted as intertidal flats than saltmarsh reveal that the diatom flora is more strongly associated with the intertidal flats than the saltmarsh. This probably reflects a greater similarity in terms of inundation frequency and as a result a greater similarity in sediment properties and salinity.

The intertidal flat habitat in Table 6.3 has a similar prediction accuracy rate to the saltmarsh, with 59% of the Samples correctly predicted. Overall, however accuracy is better with a further 31% of the Samples predicted as coming from the two neighbouring habitats of sandflat and low saltmarsh. The intertidal flat habitat type includes the muddy sandflats so the 11 samples predicted as sandflat habitats is not surprising. The sandflat habitat is the habitat with the best accuracy in prediction with 9 of the 13 samples returned as sandflat samples and the remaining four returned as intertidal flat habitats, reflecting the continuum of sand content between sandflats and muddy sandflats as well as having the same general elevation.

If sandflats and low marsh are merged with the intertidal flats habitat type, the transfer function greatly improves in predictive ability, returning a success rate of 82%. This has implications for the level of interpretation that can be obtained for fossil diatom assemblages in terms of depositional habitat, and suggests that the broader habitat groupings of intertidal flat (below to a little above MHWN) and saltmarsh (above MHWN) is highest degree of precision that should be employed with the particle-size properties of the core samples used to assist in developing a more precise prediction of the indicative depositional environment. The *Phragmites australis* category requires more samples to be added to the dataset from this habitat before the training set can be used to confidently predict this habitat from fossil diatom assemblages. However, the indicative salinity preferences of fossil assemblages together with the indicative habitat type and normalised tidal height (above MHWS for *Phragmites*) would assist in identifying samples as being indicative of the *Phragmites australis* habitat.

These results suggest that a more detailed and accurate picture of estuarine palaeoenvironmental change would be gained from predicting the fossil diatom assemblages' indicative meaning for a number of different environmental variables. Returning predictions for salinity class, normalised tidal height and habitat being the ideal.

6.6 Implications for estuarine palaeoenvironmental reconstructions

The accuracy of the transfer function developed here for predicting normalised tidal height is clearly lower than that of the regional transfer functions developed by Sherrod (1999) and Zong and Horton (1999). Small, regional datasets are much less heterogeneous that the large merged training set used here and would be expected to display a higher correlation between observed and diatom-inferred tidal height. However, whilst some regional models generated from within this dataset are shown to perform better than the global model, others perform significantly worse, (although increasing the number of samples from within a region may improve this situation). Furthermore, a regional transfer function would also encompass a smaller variety in estuarine type and ecological variables represented in the model, leading to the possibility that fossil environments are not represented in the training dataset. For example, the predictive model derived from the Humber estuary performs much better than the global model here suggesting a greater degree of the variance within this regional dataset will be explained by the individual environmental variables, as the regional element is removed. However, if such a model were to be applied to a core from the Humber estuary it would be unlikely to cover the range of past estuarine conditions experienced throughout the development of the Humber. The same would be true for the Severn, which also performs well as a regional predictive model; inevitable changes in sediment provenance over time would greatly reduce the predictive power of the model because the vast majority of contemporary Severn estuary intertidal habitats are fine-grained.

A further example of the problems incurred when regional training datasets are developed with too narrow an environmental range is given by Plater *et al.* (2000). These authors applied the diatom-based tidal level transfer function developed by Horton (1997) and Zong and Horton (1999) to a reconstruction of Holocene tidal levels and sedimentation rates in the Tees estuary. Whilst the method is sound, there is an overestimation of diatom-inferred sediment accumulation rates by a factor of three, concluded to be due to the contemporary sediment flux being an inappropriate analogue for the mid to late Holocene (Plater *et al.*, 2000).

Clearly, therefore, there is a need to find the right level of geographical trade off between capturing the higher precision of single-site based predictive models such as Sherrod (2000) and the need to cover the full range of estuarine environments likely to be represented in the palaeoestuarine record under investigation. The TWINSPAN analysis revealed a number of

groups with a strong regional affinity, e.g. the North Sea for Group Four, a grouping that also performed better than the global model. It might therefore be that this geographical scale is more appropriate.

The strong regionality displayed by the diatom data presented may have implications for the assumptions made about the cosmopolitan nature of diatom distributions. Whilst the majority of species are found throughout the study area there are a number of particular taxa that are only found in certain regions, or even certain sites. It is possible that the broad interpretations often placed on the results of local diatom studies in terms of the indicative ecological preferences and distributions of individual species should, in some instances, be re-analysed and a larger degree of regional variation in diatom floras used to characterise particular environments. Although it was only possible to elucidate a limited number of regional preferences in individual diatom species distributions in the regions-species bi-plot in Figure 6.4 (such as for *Cymatosira belgica* and *Navicula gracilis*), it is possible that with further samples added to the dataset more geographical patterns may emerge.

The variance partitioning exercise in section 6.2 revealed that, for a study area of this size and variety, the major environmental variables reflecting gradients of elevation, sediment type and salinity show only a very little inter-correlation. Horton (1997), however, did find a strong correlation between some sediment properties and elevation, specifically LOI. Horton's (1997) work is based on samples from the North Sea coast and this provides further support for the proposal that a smaller geographical scale be employed in model development to improve the signal to noise ratio.

Although the results of the variance partitioning exercise show a very low degree of relationship between the gradients of sediment properties and elevation, at a local scale the two are likely to be more closely related due to the decreasing tidal energy as the flood tide moves up over the intertidal gradient, leading to the deposition of successively finer material as the elevation increases and tidal energy reduces (see section 2.2.4). Locally, habitat type also tends to show a closer relationship to elevation than might be apparent through this broad-scale study, with vegetation colonisation exhibiting a zonation that closely follows elevation (see section 2.2.5). These inter-relationships between environmental variables is obscured in the larger dataset examined here because of the heterogeneity introduced by variation between estuaries in terms of sediment provenance, tidal regime, estuary type, salinity regime and other unmeasured variables such as eutrophication and toxic chemical

pollution. These all appear to combine to exacerbate the great variety in modern estuarine environments rather than pulling out particularly strong ecological signals for the variables of interest across the whole study area. These results suggest that a more detailed and accurate picture of estuarine palaeoenvironmental change would be gained from predicting the indicative meaning of fossil diatom assemblages for a number of different relevant environmental variables rather than concentrating solely on one (elevation).

Despite these problems discussed above, successive stages of analysis have shown that the diatom assemblages positioned at the extreme ends of some of the environmental variables measure do appear to have a higher predictive power. These include: circa MHWS and below ML in terms of normalised tidal height; high sand content in terms of sediment properties; the sandflat and general intertidal flat and high saltmarsh in terms of habitat; and the oligohaline class in terms of salinity preferences. Other similar studies have also found the upper-mid elevation (low to mid saltmarsh) diatom assemblages to be less distinctive and more mixed (e.g. Zong and Horton, 1999; Sherrod, 1999) supporting the suggestion here that it is the extremes of gradients that are more predictable. If this feature of the predictive ability of intertidal diatom assemblages is known, estuarine palaeoenvironmental reconstructions of tidal height might be interpreted with more caution and less precision, but also, ultimately, greater accuracy.

There is also a need to include more samples from environments below ML in order to improve the predictive power of the model over this part of the tidal range and reduce the effect of overestimation apparent in the model developed in section 6.4. Problems associated with obtaining such samples are discussed in section 6.4. The use of high-resolution hand-held GPS systems could make accurate elevation estimates easier to obtain for low elevation sites across a very broad intertidal zone. Furthermore, sampling methodology must be kept consistent and if low elevation mudflats are to be sample from a boat whilst the tide is in this may prove difficult. The low intertidal flats can be accessed with the use of small hovercrafts, but this is costly.

Despite the numerous issues discussed above that add to the noise within the data and bias in the tidal height predictions at upper and lower elevations, this study demonstrates a significant relationship between the distribution of estuarine diatoms in subfossil samples and the environmental gradients of elevation, salinity, sediment properties and depositional habitat. Accordingly, it should be possible to apply a more detailed large-scale predictive model to the

reconstruction of palaeotide-levels and other estuarine palaeoenvironmental variables. Although a model based on a smaller region may offer more predictive power, further research is needed to ascertain the correct geographical scale needed for the collection of a modern training dataset and this needs to be guided by the estuarine palaeoenvironment under investigation.

CHAPTER SEVEN

CONCLUSIONS

7.1 Introduction

This investigation of the use of diatoms as indicators of estuarine palaeoenvironments shows that diatom assemblages from a large dataset covering 25 intertidal Sampling Sites in Britain reveal significant patterns in the distribution of intertidal diatoms over this large geographical area. Individual Sampling Sites display strong gradients across the intertidal environment in terms of changes in the diatom subfossil assemblage composition. Cluster analysis identifies nine Groups within the diatom data, which are characterised by different habitats, sediment properties and regions of origin. Habitats with the most distinctive diatom flora include those at the extremes of the intertidal gradient. In particular a number of species show a strong association with sandflat environments. Canonical correspondence analysis has revealed that the diatom distributions have a significant relationship with elevation (measured as normalised tidal height), sediment properties, salinity, habitat and region (geographical location). Despite many diatom taxa within the dataset appearing to have a highly adaptive autecology, a large number of species show a significant distribution pattern across the tidal height gradient allowing the identification of species indicative of high, mid and low elevation environments. The significance of tidal height in terms of explaining variance within the diatom dataset justifies the development of a quantitative predictive model.

7.2 Qualitative descriptions of diatom-environment relationships

Qualitative analysis of the distribution of mean abundances of individual diatom taxa at each Site reveals strong intertidal floristic gradients at most sites. A number of species have a very widespread distribution throughout the study area, the most significant being *Rhaphoneis minutissima*, which is often associated with lower abundances of *Cymatosira belgica*. Analysis of species distributions at individual sites reveals frequent large abundances of *Rhaphoneis minutissima* across all habitats, but indicates a preference for mean elevation mudflat habitats. Other common taxa include *Achnanthes delicatula* subsp. *hauckiana*,

Navicula gregaria, Navicula perminuta, Navicula salinicola, Navicula cincta, Navicula phyllepta and *Paralia sulcata.* Habitats with more distinctive assemblages include the high saltmarsh and sandflat habitat. In every Site with a sandflat habitat this Sample displays the most unique assemblage. Mid-elevation habitats such as mid saltmarsh and low saltmarsh tend to display a less distinctive diatom assemblage that is transitional between the upper and lower elevation habitats.

Despite the clear presence of strong floristic gradients, all sites display a large degree of taphonomic over-printing, evident in the widespread distribution of epipelic and epipsammic diatoms across creek, pan and saltmarsh habitats. Species considered to be allochthonous to the intertidal environment (e.g. *Thalassiosira* spp.) also occur frequently at low abundances across all habitats. The subfossil distribution of *Paralia sulcata,* a robust species commonly found in high abundances in fossil assemblages, is interpreted as indicating an allochthonous intertidal taxa, autochthonous to the subtidal environment.

Cluster analysis using TWINSPAN identifies 9 major floristic Groups within the diatom assemblages. The composition of these Groups supports the findings of the qualitative analysis of species distributions across each site with some Groups displaying strong sandflat (low elevation) and saltmarsh (high elevation) affinities (Groups Nine and Seven respectively). Many of the mid-elevation assemblages fall into the two largest and most homogenous Groups (Three and Five) with little by way of distinctive ecological characteristics. The Sample composition of the TWINSPAN Groups reveals a strong regional character in 5 of the 9 Groups and the largest Group, Group Five, has three regional sub-groupings within it.

7.3 Variance partitioning

The series of CCAs and partial CCAs reveals that tidal height, sediment particle size and salinity account for statistically significant components of variation within the diatom dataset. Together these three variables explain 9.7% of the total variance within the diatom data with little overlap between variables. Sediment properties (4.6%) uniquely explain more variance that salinity (2.8%) and tidal height (1.9%). This low level of explained variance, both in itself and compared to other similar studies (e.g. Zong and Horton, 1999) is likely to be due to the large size and more heterogeneous nature of this dataset. Tidal height is however significant

in terms of explaining the variance within the diatom data, thus justifying the development of a predictive model for this variable.

The sandflat habitat explain a small amount of extra variance (1.5%) revealing this variable to be significant, independent of properties of grain size and elevation, supporting the conclusions from the qualitative analysis that this habitat has a particularly distinctive subfossil diatom flora.

Of the remaining variance, the regional location of the site, coded as dummy variables, explains a further 14.1%. This is a very large proportion of the variance, compared to that explained by other environmental variables and consequently a very significant and interesting result. The result reinforces and quantifies the importance of a regional overprint identified in the ecological characterisation of the TWINSPAN Groups. This importance of site location is probably due to a mixture of regional and local variation in the natural environments, and human impact. These could include phenomena such as sediment provenance, tidal energy, local climate, pollution (including organic, inorganic and directly toxic pollutants), flood-embankment development and grazing regimes, plus a whole suite of additional variables that could impact on the open water estuarine and subtidal diatom communities, and affect the nature of the autochthonous taphonomic overprinting in the subfossil assemblage.

7.4 Species distributions along the tidal gradient

The variance partitioning shows that a significant proportion of the diatom assemblage variance can be explained by normalised tidal height. Significance testing of the distribution of individual diatom species over the tidal gradient show that most individual taxa also display a significant relationship to tidal height. This offers further justification for the development of a predictive model based on normalised tidal height. Analysis of the distribution curves, weighted average optima and tolerances for individual species highlights a number of species that have a strong association with the ends of the tidal height gradient. Species found to be indicative of the low end of the tidal gradient include *Amphora wiseii*, *Cocconeis neothumensis, Cocconeis scutellum* and *Navicula germanopolonica.* Species found to be indicative of the top end of the tidal gradient include *Denticula sundaysensis*, *Navicula cincta* and *Navicula mutica.* A large number of taxa have wide tolerances and

optima towards the middle of the tidal range gradient. Many of the species showing no significant distribution along the tidal gradient are allochthonous planktonic forms such as *Actinocyclus senarius* and *Thalassiosira* species. Species with no significant distribution should not have any biasing impact on tidal height predictions and as such this finding supports the assertion discussed by Sherrod *et. al* (1989) that the analysis of subfossil diatom assemblage composition for the purpose of predicting estuarine environmental variables should not involve the separation of autochthonous and allochthonous taxa as the latter are an integral component of the resultant fossil assemblage.

7.5 Diatom based tidal height calibration model

The apparent and jack-knifed diatom based tidal calibration models show a clustering of predictions around the middle of the tidal gradient. This reflects the distribution of Samples within the training dataset but has implications for the predictions of Samples from the ends of the tidal gradient. RMSE and r^2 values for the apparent predicted values are 0.259 and 0.61 respectively whilst the $RMSE_{jack}$ and r^2 for the jack-knifed model are 0.338 and 0.35. Prediction errors are higher in the jacknifed model, as would be expected, but this is a more realistic reflection of the predictive power of the model when applied to fossil diatom assemblages. The errors of prediction are found to be worse than those for other similar transfer functions such as those developed by Sherrod (1999) and Zong and Horton (1999). This poor performance is concluded to be due to the merging of data from a large number of sites over a large geographical area. Such merging has apparently introduced a large amount of noise into the diatom / elevation relationship, and is probably related to the increased heterogeneity and interaction of the sediment type and elevation, and the observed regional overprint in the diatom assemblages.

A series of predictive models developed from individual regional dataset and regional groupings returned the same number of regional models with a better performance than the global model as returned with a poorer performance. Those regional that were found to perform better than the global model include: the Humber; the Severn; The Solway; the South East; the East Coast grouping; the Northern Regions grouping; and the Severn and South East. However, none of these regional models on their own contain enough samples to provide the basis for a sufficiently detailed training dataset to apply to palaeoenvironmental reconstructions.

Analogue matching to infer Sample habitats from the diatom data performs with a success rate of 59%. The majority of habitats predicted incorrectly are predicted as habitats with a close ecological character, in terms of sediment properties and elevation, to the actual Sample habitat. Further merging of the habitat types based on these ecologically similarities increases the success rate to 82%.

The most significant finding of this study is the large amount of diatom variance explained by the variable of regions. This has a number of implications for the application of large geographical scale transfer functions to sea level reconstructions and the reconstruction of other aspects of the estuarine palaeoenvironments. Although predictive models generated from some regions were found to perform better than the global model, the correct scale of trade off between coverage of palaeoenvironments and fossil diatom species, and reduction of regionality in the modern training dataset, is an issue that needs further research. A more detailed transfer function developed for the North Sea coast would be a very good starting point to test these issues due to the strong regional character of Samples from this area and the better performance of the East Coast (North Sea) model compared to the global model. Other sub-regions within this dataset that might lend themselves to the development of a more detailed transfer function, based on the TWINSPAN Group preferences in Chapter Five, the regions-species bi-plot and the regional predictive models, could be northern and southern Britain. The work of Horton (1997) and Zong and Horton (1999) suggest that a North Sea or northern Britain approach does provide a more precise model with elevation having a greater degree of significance and this is supported by this study as both the East Coast regional model and the Northern regional model improve on the performance of the global model.

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APPENDIX 1

Categorisation of samples from vegetated habitats according to the National Vegetation Classification (Rodwell, 2000)

Sample	NVC community code	NVC Community Name	NVC subcommunity
AM1	SM13	Puccinellia maritima saltmarsh community	
AM2	SM14	Halimione portulacoides saltmarsh community	
AM4	SM8	Annual Salicornia saltmarsh community	
AM5	SM6	Spartina anglica saltmarsh community	
AU1	SM6	Spartina anglica saltmarsh community	
AU2	SM6	Spartina anglica saltmarsh community	
AU3	SM6	Spartina anglica saltmarsh community	
AU6	SM13	Puccinellia maritima saltmarsh community	
BB1	SM16	Festuca rubra saltmarsh community	Puccinellia maritima dominant subcommunity
BB2	SM13	Puccinellia maritima saltmarsh community	Limonium vulgare - Armeria maritima subcommunity
BB3	SM6	Spartina anglica saltmarsh community	
BB4	SM6	Spartina anglica saltmarsh community	
BB7	S4	Phragmites australis swamp	
BH2	SM14	Halimione portulacoides saltmarsh community	
BH4	SM8	Annual Salicornia saltmarsh community	
BK3	S21	Suaeda vera-Limonium binervosum saltmarsh community	
BK4	S4	Phragmites australis swamp	
BK5	S4	Phragmites australis swamp	
BS1	SM16	Festuca rubra saltmarsh community	Festuca rubra-Glaux maritima subcommunity
BS3	SM16	Festuca rubra saltmarsh community	Festuca rubra-Glaux maritima subcommunity
CK3	SM8	Annual Salicornia saltmarsh community	
CK5	SM16	Festuca rubra saltmarsh community	Festuca rubra-Glaux maritima subcommunity
CK6	SM28	Elymus repens saltmarsh community	
DB1	SM6	Spartina anglica saltmarsh community	
DB3	SM8	Annual Salicornia saltmarsh community	
FR2	SM8	Annual Salicornia saltmarsh community	
FR3	SM8	Annual Salicornia saltmarsh community	
FR4	SM14	Halimione portulacoides saltmarsh community	

Appendix 1 continued

Sample	NVC community code	NVC Community Name	NVC subcommunity
FR5	SM10	Transitional low-marsh vegetation with Puccinellia maritima, annual Salicornia species and Suaeda maritima	
FR6	SM13	Puccinellia maritima saltmarsh community	
GP1	SM13	Puccinellia maritima saltmarsh community	
GP3	SM14	Halimione portulacoides saltmarsh community	
HI1	SM13	Puccinellia maritima saltmarsh community	
HI2	SM13	Puccinellia maritima saltmarsh community	
HI3	SM13	Puccinellia maritima saltmarsh community	
HI4	SM13	Puccinellia maritima saltmarsh community	
HI5	SM13	Puccinellia maritima saltmarsh community	
HI6	SM8	Annual Salicornia saltmarsh community	
HW2	SM6	Spartina anglica saltmarsh community	
HW3	SM9	Suaeda maritima saltmarsh community	
HW4	SM9	Suaeda maritima saltmarsh community	
HW7	SM24	Elymus pycnanthus saltmarsh community	
LY2	SM8	Annual Salicornia saltmarsh community	
LY3	SM14	Halimione portulacoides saltmarsh community	
LY4	SM14	Halimione portulacoides saltmarsh community	
MD5	SM9	Suaeda maritima saltmarsh community	
MD6	SM6	Spartina anglica saltmarsh community	
MD7	MG11	Festuca rubra-Agrostis stolonifera-Potentilla anserina inundation community	Lolium perenne subcommunity
PH1	S4	Phragmites australis swamp	
PH2	S4	Phragmites australis swamp	
SB2	SM16	Festuca rubra saltmarsh community	Festuca rubra-Glaux maritima subcommunity
SH1	SM14	Halimione portulacoides saltmarsh community	
SH2	SM13	Puccinellia maritima saltmarsh community	
SH4	SM13	Puccinellia maritima saltmarsh community	Puccinellia maritima dominant
SH5	SM8	Annual Salicornia saltmarsh community	
SH7	SM8	Annual Salicornia saltmarsh community	
SK3	SM8	Annual Salicornia saltmarsh community	
SK5	SM13	Puccinellia maritima saltmarsh community	Limonium vulgare-Armeria maritima subcommunity
SK7	SM13	Puccinellia maritima saltmarsh community	Limonium vulgare-Armeria maritima subcommunity

Appendix 1 continued

Sample	NVC community code	NVC Community Name	NVC subcommunity
SM1	SM14	Halimione portulacoides saltmarsh community	
SM2	SM6	Spartina anglica saltmarsh community	
WK5	SM6	Spartina anglica saltmarsh community	
WK6	SM14	Halimione portulacoides saltmarsh community	
WK7	SM13	Puccinellia maritima saltmarsh community	Puccinellia maritima dominant subcommunity
WL5	SM13	Puccinellia maritima saltmarsh community	Limonium vulgare-Armeria maritima subcommunity
WL6	SM27	Ephemeral saltmarsh vegetation with Sagina maritima	
WT3	SM11	Aster tripolium var. discoides saltmarsh community	
WT4	SM13	Puccinellia maritima saltmarsh community	Puccinellia maritima dominant subcommunity
WT5	SM15	Juncus maritimus-Triglochin maritima saltmarsh community	
WT6	SM28	Elymus repens saltmarsh community	
AM1	SM13	Puccinellia maritima saltmarsh community	
AM2	SM14	Halimione portulacoides saltmarsh community	
AM4	SM8	Annual Salicornia saltmarsh community	

APPENDIX 2

Diatom taxa greater than 2% abundance, showing number of occurrences (N), maximum abundance, and Hill's N_2.

Taxon #	Taxon name	Author	Year	N	Max	N2
AXX685	Achnanthes delicatula subsp. engelbrechtii	Cholnoky, Lange-Bertalot	1981	15	3.40	7.43
AC156A	Achnanthes amoena	Hustedt	1952	36	2.01	22.33
AC058B	Achnanthes brevipes var. brevipes	Ag.	1824	19	3.11	8.12
XXX555	Achnanthes c.f. helvetica	(Hustedt) Lange-Bertalot & Krammer	1980	24	2.44	15.58
AC016A	Achnanthes delicatula	Kutz.		20	3.70	11.71
XXX567	Achnanthes delicatula (small)			15	4.66	7
XXX565	Achnanthes delicatula subsp. aff.engelbrechtii	sensu Krammer and lange-Bertalot	1991	9	18.92	3.93
AC016B	Achnanthes delicatula subsp. delicatula	(Kutz.) Grun. in Cleve & Grun.	1880	49	10.26	18.27
AC016C	Achnanthes delicatula subsp. hauckiana	(Grun. in Cleve & Grun.) Lange-Bertalot & Rumrich	1990	100	21.15	33.23
XXX998	Achnanthes delicatula subsp. septentrionalis	(Oestrup) Lange-Bertalot in Lange-Bertalot & Krammer	1993	8	2.39	2.62
AC074A	Achnanthes groenlandica	(Cleve) Grun. in Cleve & Grun.	1880	1	5.51	1
AC001A	Achnanthes lanceolata	(Breb. ex Kutz.) Grun. in Cleve & Grun.	1880	22	8.58	2.76
AC047A	Achnanthes lauenburgiana	Hust.	1933	36	15.15	11.5
AC013A	Achnanthes minutissima	Kutz.	1833	47	2.62	27.68
AT010A	Actinocyclus senarius	Ehrenb.	1938	62	2.39	34.21
AP002A	*Amphipleura rutilans*	(Trentepohl ex Roth) Cleve	1894	52	8.70	19.38
XXX696	Amphora abludens	Simonsen	1960	28	18.30	4.39
AM002A	Amphora acutiuscula	Kutz.	1844	71	7.47	28.13
AM022A	*Amphora arenaria*	Donk.	1855	1	2.61	1
XXX550	Amphora c.f. delicatissima	Kasske ex Hustedt	1930	59	3.21	34.9
AM006D	Amphora coffeaeformis var. aponina	(Kutz.) Archibald & Schoeman	1983	8	2.31	4.3
AM006A	*Amphora coffeaeformis* var. coffeaeformis	(Ag.) Kutz.	1844	45	12.27	9.69
XXX653	Amphora coffeiformis	(Kutzing) Schoemann & Archibald	1986	34	6.32	11.52
AM010A	Amphora fogediana	Krammer	1985	31	4.79	10.1
AM012A	*Amphora pediculus*	(Kutz.) Grun.		42	10.29	7.41
XXX385	Amphora tenuissima	Hustedt	1955	37	5.23	17.34
XXX986	Amphora wiseli	(Sataln) Simonsen	1982	13	13.33	3.13
XXX652	Biremis lucens	(Hustedt) Sabbe, Witkowski & Vyverman	1995	73	28.91	13.42
XXX505	Biremis sp. A			18	2.20	8.28
XXX389	c.f. Paralia sulcata	(Grunow) Round & Basson	1997	30	8.15	11.59
CA002A	Caloneis bacillum	(Grun.) Cleve	1894	29	3.42	14.67
XXX538	Caloneis sp. A			22	16.60	6.87
CA046A	Caloneis westii	(W. Sm.) Hendey	1964	19	3.95	6.95
CPS02A	*Campylosira cymbelliformis*	(A. Schmidt) Grun. ex Van Heurck	1885	54	4.82	23.47
CTE01A	Catenula adhaerens	(Mereschk.) Mereschk.	1903	67	21.10	10.87
CO024A	Cocconeis distans	Greg.	1855	9	3.11	3.62
XXX395	Cocconeis hauniensis	Witkowski	1993	10	2.87	4.19
XXX973	Cocconeis hoffmanii	Simonsen	1959	17	4.76	5.8
XXX477	Cocconeis neodimunata			23	4.13	10.7
XXX972	Cocconeis neothumensis	Krammer	1991	24	5.45	9
CO049A	Cocconeis peltoides	Hust.	1939	52	4.93	20.71
CO007A	Cocconeis scutellum	Ehrenb.	1838	53	28.54	8.08
CY003A	Cyclotella meneghiniana	Kutz.	1844	25	3.08	8.7
CT001A	Cymatosira belgica	Grun. in Van Heurck	1881	77	30.45	34.11
DEL01A	Delphineis surirella	(Ehrenb.) G. Andrews	1981	74	7.28	33.78
XXX649	Denticula subtilis	Grunow	1862	36	18.55	10.7
XXX399	Denticula sundaysensis	Archibald	1982	15	18.98	3.67

Appendix 2 continued

[illegible]	Taxon name	[illegible]	[illegible]	[illegible]	[illegible]
DP013A	Diploneis aestuari	[illegible]	1969	24	2.79	12.57
DP030A	Diploneis didyma	(Ehrenb.) Cleve	1894	16	4.33	6.23
XXX680	Diploneis interrupta	(Kutzing) Cleve	1894	4	2.76	1.46
XXX410	Diploneis modica	Hustedt	1945	4	4.00	1.32
DP001A	Diploneis ovalis	(Hilse) Cleve	1894	18	2.38	11.2
XXX473	Entomoneis glaucosa var. subsalina	(Cleve) Krammer	1986	7	2.65	3.77
XXX682	Fallacia bassoliae	Witkowski	1981	20	14.29	6.35
FA004A	Fallacia cryptodyra	(Brockmann) Stickle & Mann	1990	12	11.11	3.27
FA007A	Fallacia forcipata	(Greville) Stickle & Mann	1990	27	5.51	10.02
XXX960	Fallacia pseudony	(Hustedt) Mann in Round et al	1990	10	2.97	4.05
FA001A	Fallacia pygmaea	(Kutz.) Stickle & Mann	1990	47	6.94	17.02
FA023A	Fallacia tenera	(Hust.) Mann	1990	22	6.94	8.11
FR025A	Fragilaria atomus	Hust.	1931	49	16.17	9.32
FR009A	Fragilaria capucina var. capucina	Desm.	1825	12	3.18	3.55
FR009B	Fragilaria capucina var. mesolepta	(Rabenh.) Rabenh.	1864	2	2.53	1.17
XXX406	Fragilaria cassubica	Witkowski et Lange-Bertalot	1993	27	13.17	5.94
FR018A	Fragilaria elliptica	Schum.	1867	31	2.21	15.54
XXX658	Fragilaria exigua	Grunow in Cleve and Moller	1878	18	2.99	7.9
XXX681	Fragilaria famelica	(Kutzing) Lange-Bertalot	1980	13	4.79	4.23
FR001A	Fragilaria pinnata	Ehrenb.	1843	38	3.70	14.98
FR047A	Fragilaria schulzii	Brockm.	1950	18	10.77	3.93
FU019A	Frustulia linkei	Hust.	1952	8	4.77	3.62
GO038A	Gomphonema exiguum	Kutz.	1844	1	4.40	1
GO013A	Gomphonema parvulum	(Kutz.) Kutz.	1849	14	2.40	6.93
XXX625	Gomphonemopsis exigua var. exigua	Medlin	1986	7	4.61	2.02
GR007A	Grammatophora oceanica fo. subtilissima	(J.W. Bail. ex Ralfs in Pritch.) Hust.	1931	2	2.36	1.71
GY013B	Gyrosigma distortum var. distortum	(W. Sm.) Griffith & Henfrey	1856	16	3.48	8.9
GY014A	Gyrosigma eximium	(Thwaites) Boyer	1927	35	20.84	6.9
GY003A	Gyrosigma fasciola	(Ehrenb.) Griffith & Henfrey	1856	20	2.04	10.95
XXX691	Gyrosigma litorale	(W. Smith) Cleve	[illegible]	9	11.16	2.1
GY021A	Gyrosigma peisonis	(Grun.) Hust.	1930	66	8.17	30.43
GY025A	Gyrosigma scalproides	(Rabenh.) Cleve	1894	9	3.61	4.22
MA014A	Mastogloia exigua	Lewis	1861	6	5.53	1.56
ME007A	Melosira nummuloides	Ag.	1824	1	2.82	1
XXX401	Navicula abscondita	Hustedt	1939	27	14.31	6.36
NA220A	Navicula arenaria	Donk.	1861	25	67.61	1.45
XXX697	Navicula bergii	(Krasske) Krasske	1932	18	2.57	6.53
XXX419	Navicula bobustuata	A. Mann	[illegible]	20	8.00	6.82
NA099A	Navicula bremensis	Hust.	1957	8	8.68	2.03
XXX396	Navicula c.f. flagellifera	Hustedt	1939	64	18.49	17.56
XXX618	Navicula c.f. microcari	Lange-Bertalot	1993	21	5.79	7.57
XXX571	Navicula c.f. palpebralis	Brebisson ex. W. Smith	1953	40	3.42	21.23
NA021A	Navicula cincta	(Ehrenb.) Ralfs in Pritch.	1961	76	61.22	18
XXX639	Navicula cruezbergensis	Krasske	1957	16	3.74	6.92
NA751A	Navicula cryptotenella	Lange-Bertalot	1985	8	2.40	4.7
NA060A	Navicula digito-radiata var. digito-radiata	(Greg.) Ralfs in Pritch.	1861	56	4.79	22.4
XXX688	Navicula digito-radiata var. minima	Cleve-Euler	1953	50	13.24	19.83
NA336A	Navicula dissipata	Hust.	1942	8	2.94	3.19
NA359A	Navicula finmarchica	(Cleve & Grun.) Cleve	1896	14	8.25	2.64
NA363B	Navicula flanatica	Grun.	1960	50	8.92	14.1

Appendix 2 continued

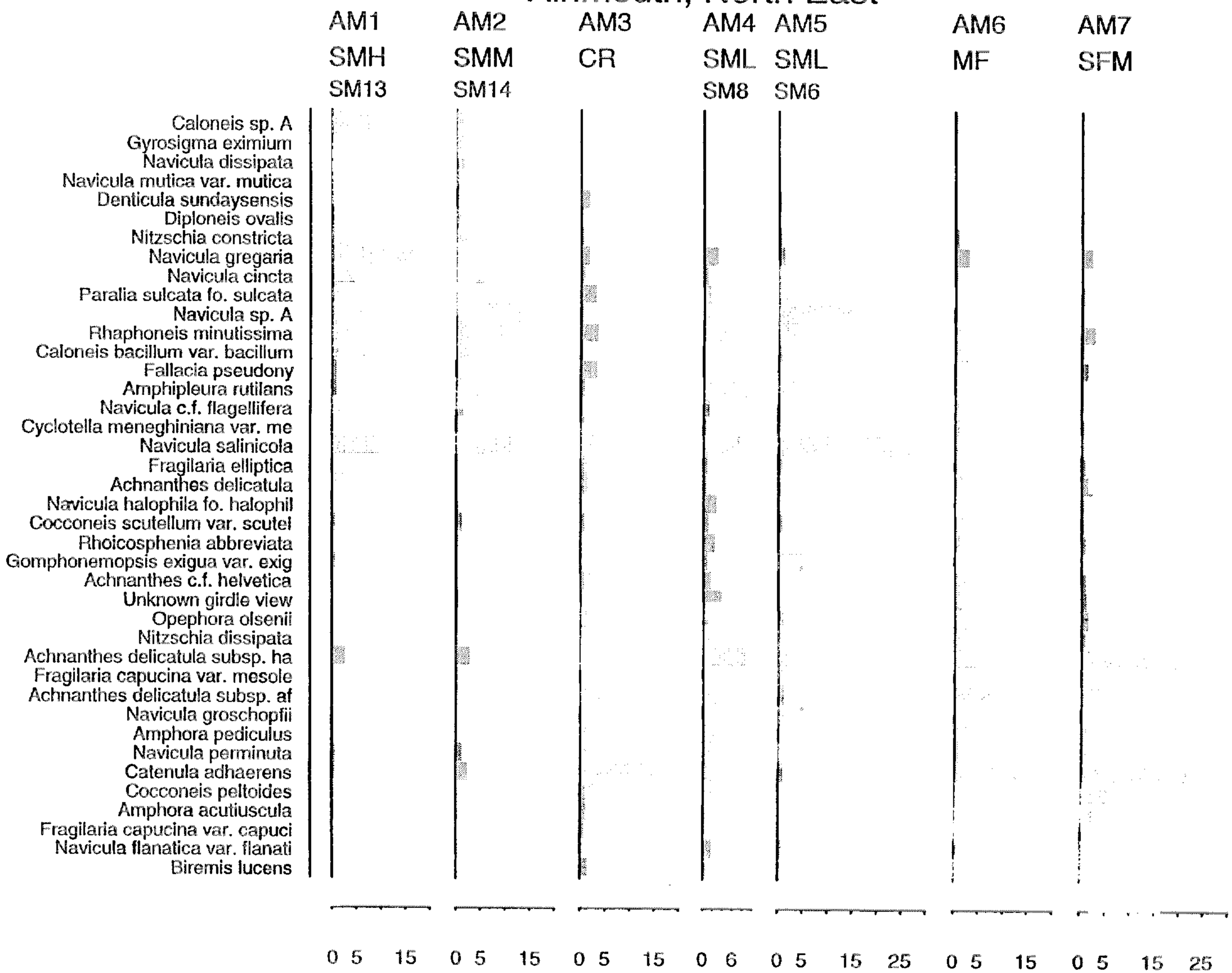
Taxon code	Taxon name	Author	Year	n	Mean	SD
XXX631	Navicula germainopsoides	Witkowski & Lange-Bertalot in Lange-Bertalot	1993	71	24.85	17.35
NA029A	Navicula gracilis	Ehrenb.	1830	15	10.10	4.73
NA023A	Navicula gregaria	Donk.	1861	89	44.44	28.64
NA011A	Navicula grischopfii	Hust.	1939	30	4.84	17.59
NA022A	Navicula halophila	(Grun. ex Van Heurck) Cleve	1894	50	22.17	12.52
XXX695	Navicula heterovalvata	Simonsen	1959	23	8.28	7.53
NA436D	Navicula ignota var. acceptata	(Hustedt) Lange-Bertalot	1985	21	2.42	11.94
NA743A	Navicula lucinensis	Hustedt	1930	4	5.39	2.46
NA809A	Navicula menadana	Hendey	1958	44	8.33	15.15
NA030A	Navicula menisculus	Schum.	1867	6	3.41	2.39
NA035A	Navicula meniscus	Schum.	1867	28	5.43	10.56
XXX623	Navicula microdigitoradiata	Lange-Bertalot	1993	61	26.80	23.1
NA025A	Navicula mutica var. mutica	Kutz.	1844	36	11.19	9.79
XXX594	Navicula nolens	Simonsen	1959	27	7.16	9.81
NA062A	Navicula perdebralis	Bock ex W. Sm.	1853	38	3.99	14.8
XXX699	Navicula pau-sanuzii	Witkowski et Lange-Bertalot	1994	37	5.47	18.94
NA555A	Navicula pavillardii	Hust.	1939	28	4.56	13.78
NA564A	Navicula perirepida	Grun.	1884	1	7.41	1
NA565A	Navicula perminuta	Grun. in Van Heurck	1880	105	33.95	39.05
NA058A	Navicula phyllepta	Kutz.	1844	88	30.80	33.69
XXX531	Navicula praestoeensis	Moller	1950	43	18.36	13.92
NA578A	Navicula praeterita	Hust.	1945	17	3.40	9.15
NA047A	Navicula protracta	Grun. in Cleve & Grun.	1880	31	3.00	14.59
NA059A	Navicula ramosissima	(Ag.) Cleve	1895	38	8.92	16.91
NA035A	Navicula salinarum	Grun. in Cleve & Grun.	1880	15	5.60	4.72
NA514A	Navicula salinicola	Hust.	1939	98	26.96	46.33
NA005A	Navicula seminulum	Grun.	1860	7	3.58	2.25
XXX643	Navicula sp. A			61	16.02	26.89
XXX637	Navicula sp. B			23	2.59	10.33
XXX631	Navicula sp. C			12	2.23	6.59
XXX420	Navicula stanmarchii	Witkowski et Lange-Bertalot		22	4.29	9.71
XXX690	Navicula subminiscula	Manguin	1941	7	2.90	4.75
NA675A	Navicula tenelloides	Hust.	1937	22	3.75	11.31
NA533A	Navicula transitans	Cleve	1883	40	3.42	18.74
NA033A	Navicula trivialis	Lange-Bertalot	1980	20	9.00	6.11
NI040A	Nitzschia acuminata var. acuminata	(W. Sm.) Grun.	1878	23	5.91	7.29
NI040B	Nitzschia acuminata var. subconstricta	Grun. in Cleve & Grun.	1880	2	2.68	1.15
NI063A	Nitzschia agnita	Hust.	1957	3	5.45	1.72
NI028A	Nitzschia capitellata	Hust.	1930	56	10.96	15.58
NI060A	Nitzschia clausii	Hantzsch	1860	25	11.90	5.16
XXX614	Nitzschia coarctata	Grunow in Cleve & Moller	1878	48	3.71	24.13
NI200A	Nitzschia compressa	(Bailey) Boyer	1916	20	5.45	6.4
NI083A	Nitzschia constricta	(Kutz.) Ralfs in Pritch.	1861	77	20.47	26.44
NI088A	Nitzschia debilis	Grun. in Cleve & Grun.	1880	25	13.88	8.18
NI015A	Nitzschia dissipata	(Kutz.) Grun.	1862	78	10.51	29.43
XXX391	Nitzschia fontifuga	Cholnoky	1932	76	12.28	31.2
NI008A	Nitzschia frustulum	(Kutz.) Grun. in Cleve & Grun.	1880	60	4.35	27.97
NI203A	Nitzschia liebetruthii	Rabenhorst	1864	35	4.24	19.87
NI131A	Nitzschia lorenziana	Grun. in Cleve & Grun.	1880	9	4.63	2.2
NI027A	Nitzschia microcephala	Grun. in Cleve & Grun.	1880	22	15.84	5.94

Appendix 2 continued

Taxonomic	Taxonomic	Author	Yr		Max	A2
N0224A	Nitzschia navicularis	(Breb. ex Kutz.) Grun. in Cleve & Grun.	1860	18	12.99	1.96
N0036A	Nitzschia palea var. palea	(Kutz.) W. Sm.	1853	31	2.83	18.88
N0098A	Nitzschia sigma	(Kutz.) W. Sm.	1853	66	7.99	22.42
XXX495	Nitzschia sp. A			9	2.22	4.02
XXX098	Nitzschia thermalbides	Hustedt	1955	33	5.13	10.8
N0048A	Nitzschia tubicola	Grun. in Cleve & Grun.	1880	15	3.35	8.72
N0138A	Nitzschia valdestriata	Aleem & Hust.	1951	10	3.93	3.12
OD001A	Odontella aurita	(Lyngb.) Ag.	1832	57	5.71	20.85
XXX904	Opephora krasskeana	Witkowski	1994	17	2.40	7.94
XXX525	Opephora marina var. minuta	Cleve-Euler	1953	30	16.36	7.54
XXX903	Opephora olsenii	Moller	1950	54	3.43	24.12
OP005A	Opephora parva	(Grun. in Van Heurck) Krasske	1939	42	3.56	20.62
PA001A	Paralia sulcata	(Ehrenb.) Cleve	1873	83	12.35	33.51
PI047A	Pinnularia intermedia	(Lagerst.) Cleve	1896	4	2.79	2.36
XXX409	Pinnularia krookiformis	Krammer	1992	1	3.39	1
PF005A	Plagiogramma laeve	(Greg.) *Ralfs in Pritch.*	1861	70	16.70	23.81
XXX398	Plagiogramma pulchella	Greville		29	13.60	7.65
PF011A	Plagiogramma van-heurckii	Grun. in Van Heurck	1881	66	17.20	12.92
XXX387	Plagiogrammopsis crawfordii	Witkowski, Lange-Bertalot & Metzelin	2000	44	7.49	13.08
PG008A	Plagiotropis vitrea	(W. Sm.) Grun. in Cleve & Grun.	1880	35	2.06	20.85
XXX384	Planothidium oberdanum	(Griffen) Witkowski, Lange-Bertalot & Metzelin	2000	21	3.20	11.2
PL033A	Pleurosigma marinum	Donk.	1858	15	3.42	4.52
XXX390	Pseudostaurosira perminuta	(Grunow) Sabbe & Vyreman	1995	21	9.20	7.14
RA007A	Rhaphoneis minutissima	Hust.	1939	112	43.95	63.97
RC002A	Rhoicosphenia abbreviata	(Ag.) Lange-Bertalot	1980	22	2.17	12.66
XXX896	Rhopalodia constricta	(W. Smith) Krammer	1987	2	5.73	1.57
SC004A	Scoliopleura tumida var. adriatica	(Grun.) H. & M. Perag.	1898	6	3.92	2.93
SC004B	Scoliopleura tumida var. tumida	(Breb. ex Kutz.) Rabenh.	1864	9	3.68	2.67
SA021A	Stauroneis amphioxys	Greg.	1856	8	2.23	3.45
SA063A	Stauroneis salina	W. Sm.	1853	60	13.56	14.43
TU003A	Tabularia fasciculata	(Ag.) Williams & Round	1986	32	2.63	15.08
XXX893	Tabularia tabulata	(C. A. Agardh) Snoeijs	1992	23	14.76	2.22
TH026A	Thalassiosira oestrupii	(Ostenf.) Hasle	1972	43	5.30	17.07
XXX693	Thalassiosira proschkinae	Makarova	1979	41	4.25	18.8
TH031A	Thalassiosira pseudonana	(Hust.) Hasle & Heimdal	1970	25	5.91	11.6
XXX483	Unknown girdle view			15	3.48	9.95

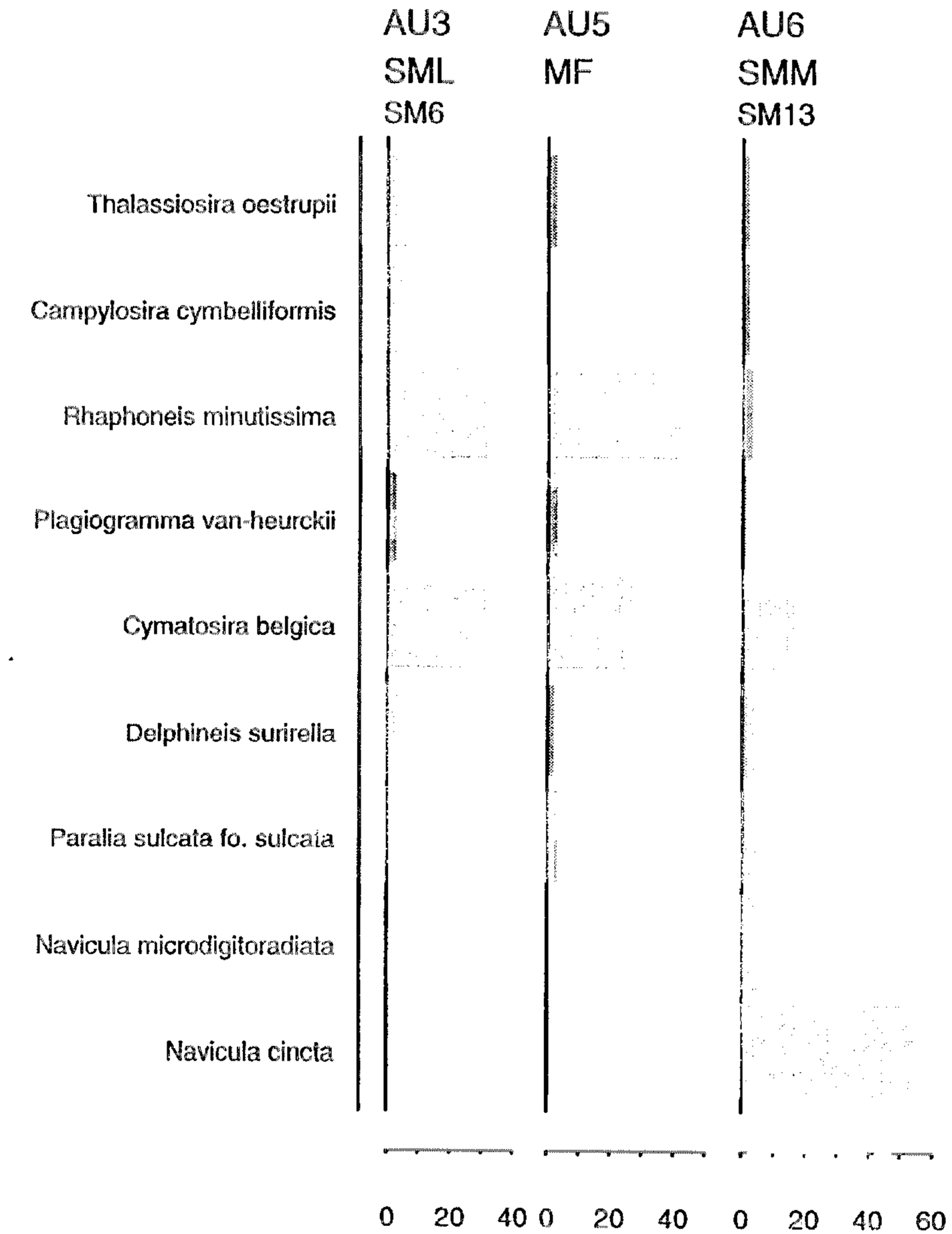
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Alnmouth, North East



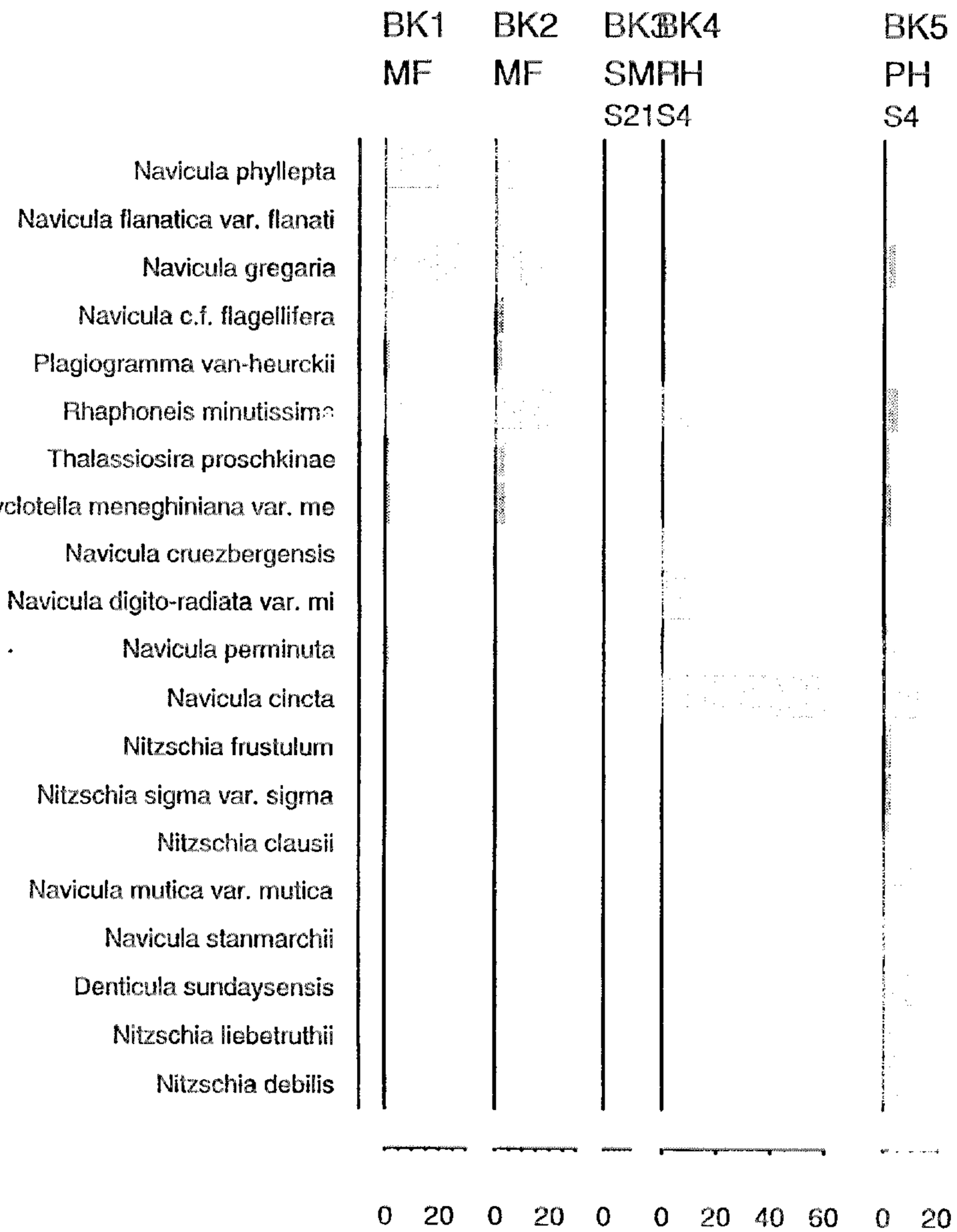
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Aust, Severn Estuary



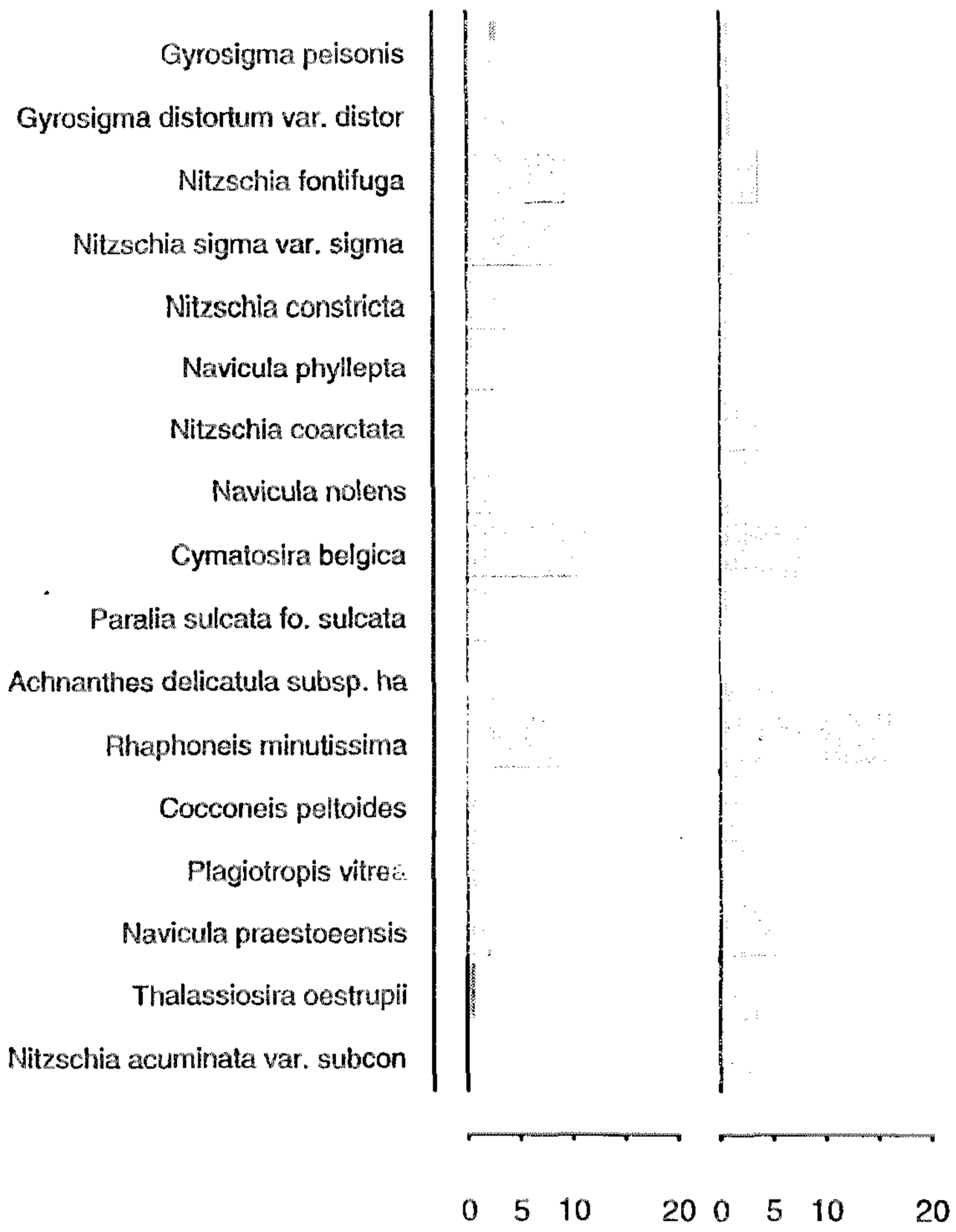
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Blacktoft Sands, Humber



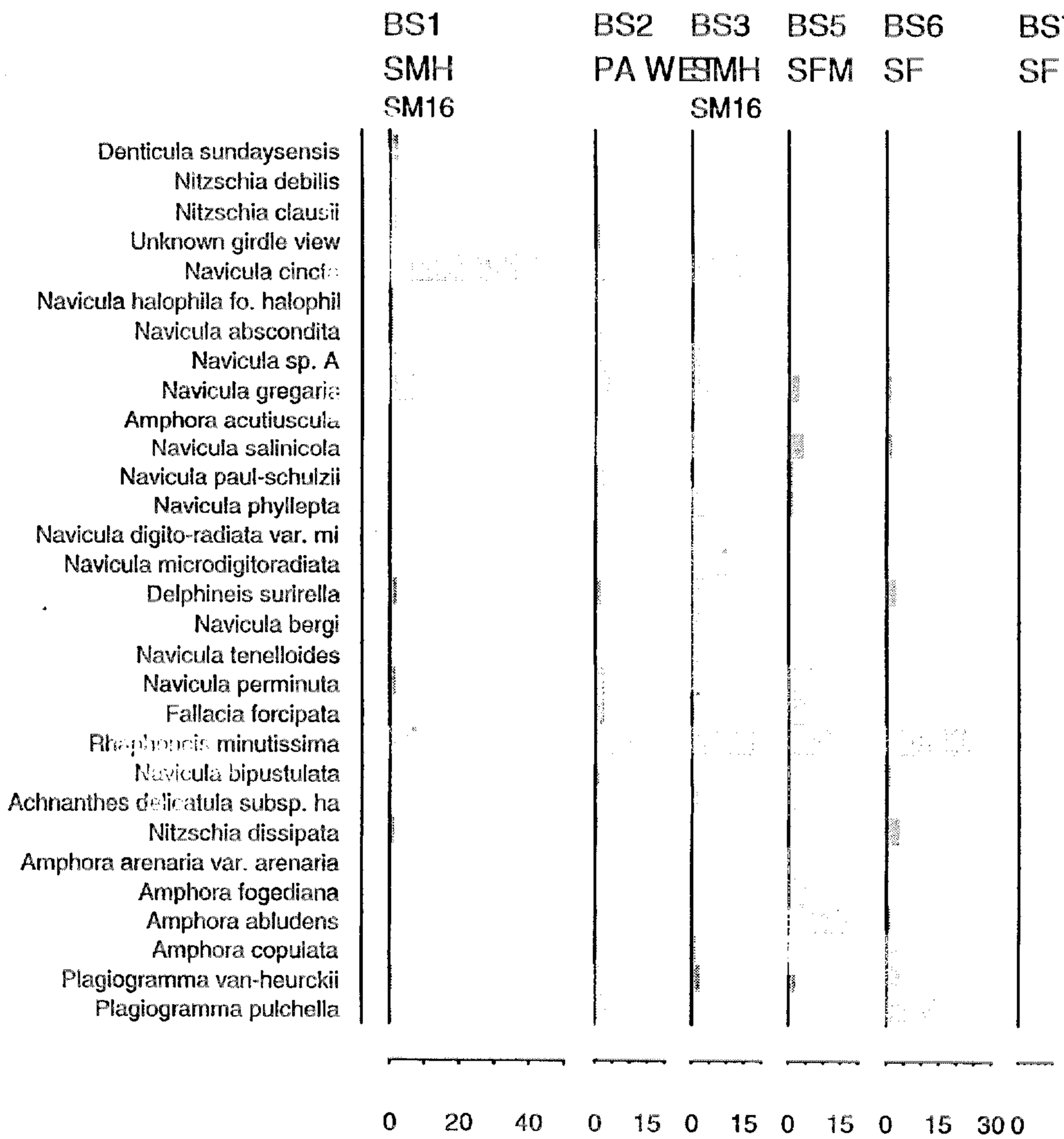
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Blackwater, South East Anglia



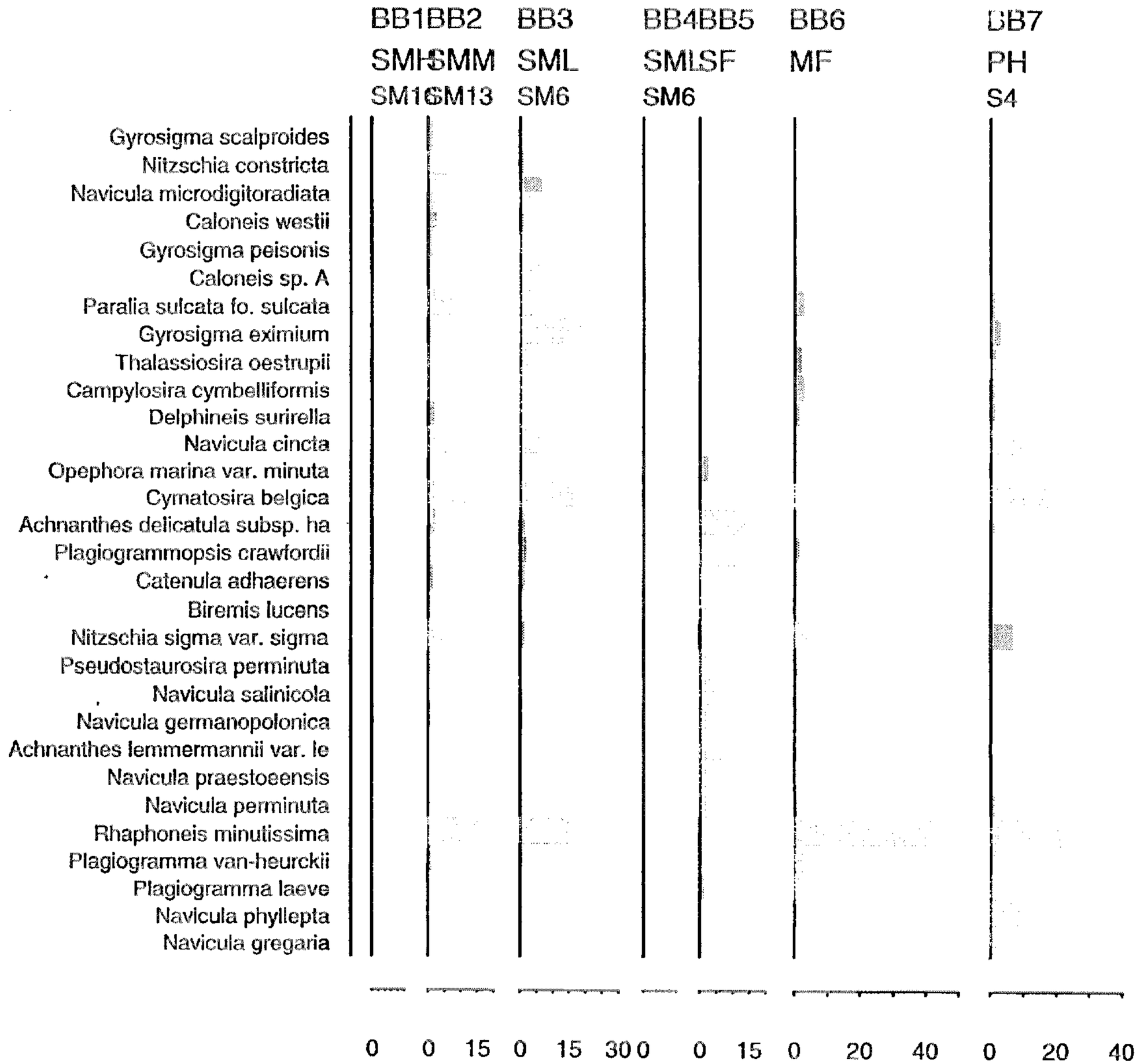
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Bowness, Solway Firth



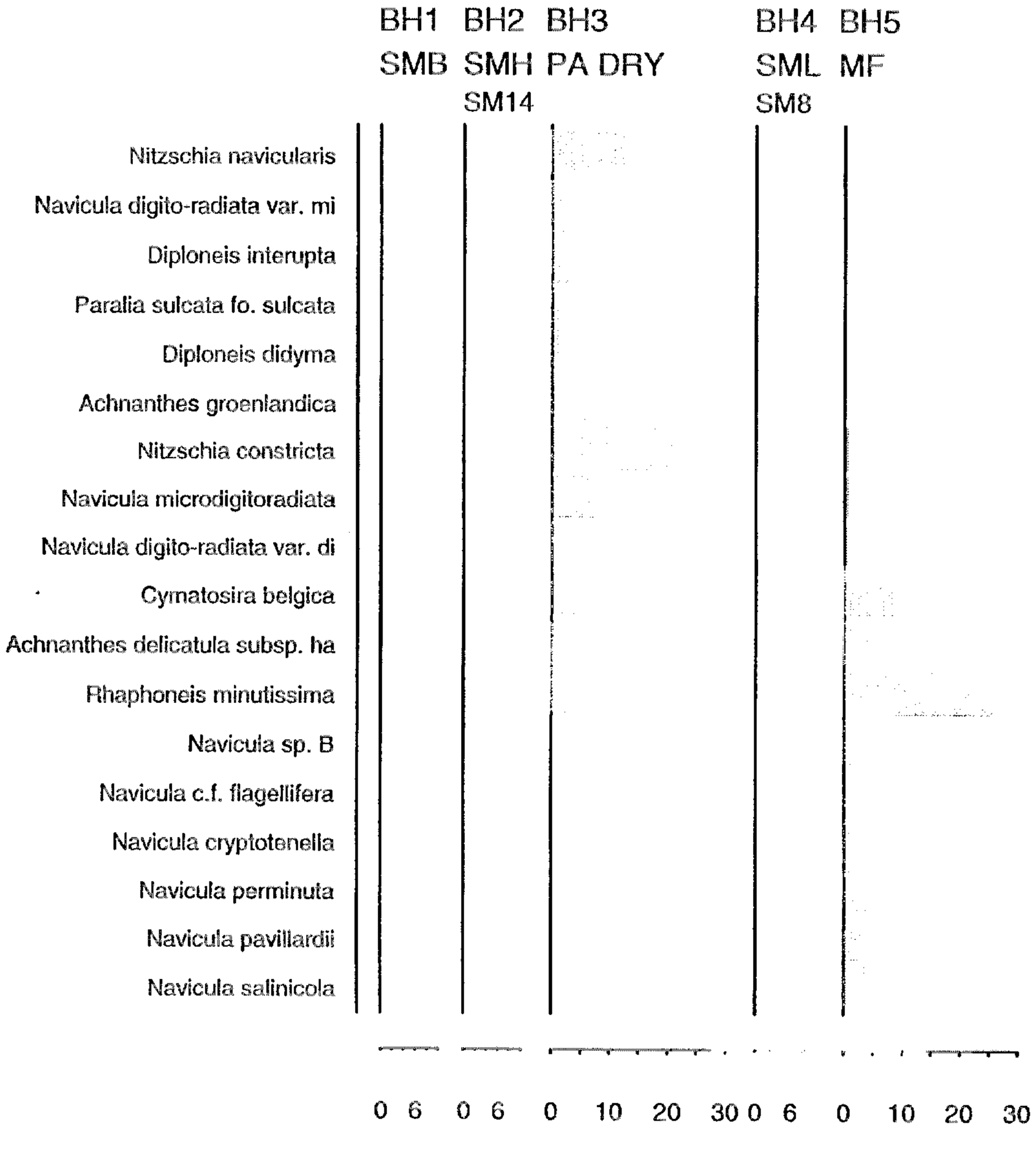
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Bridgewater Bay, Severn Estuary



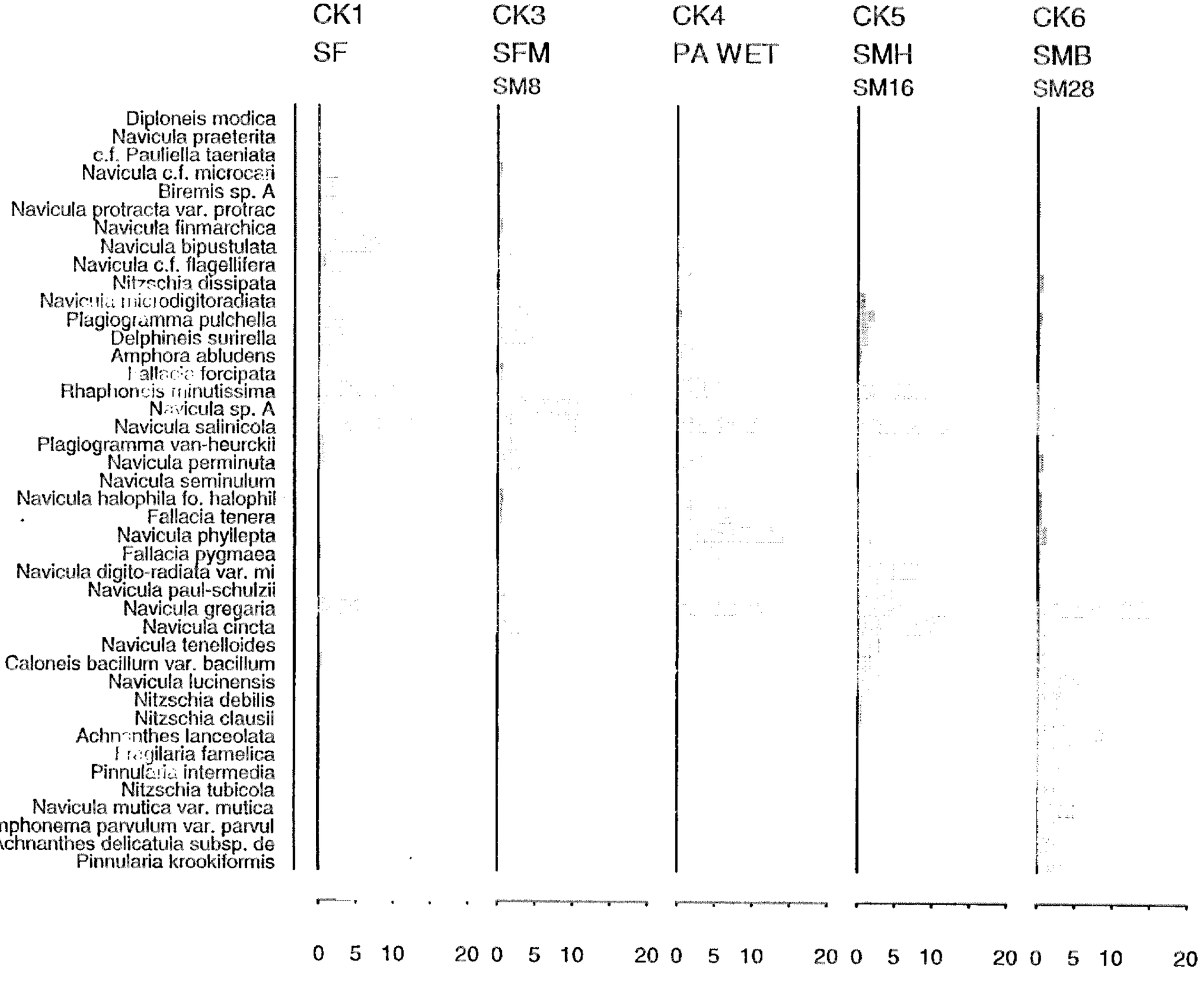
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Burnham, Norfolk



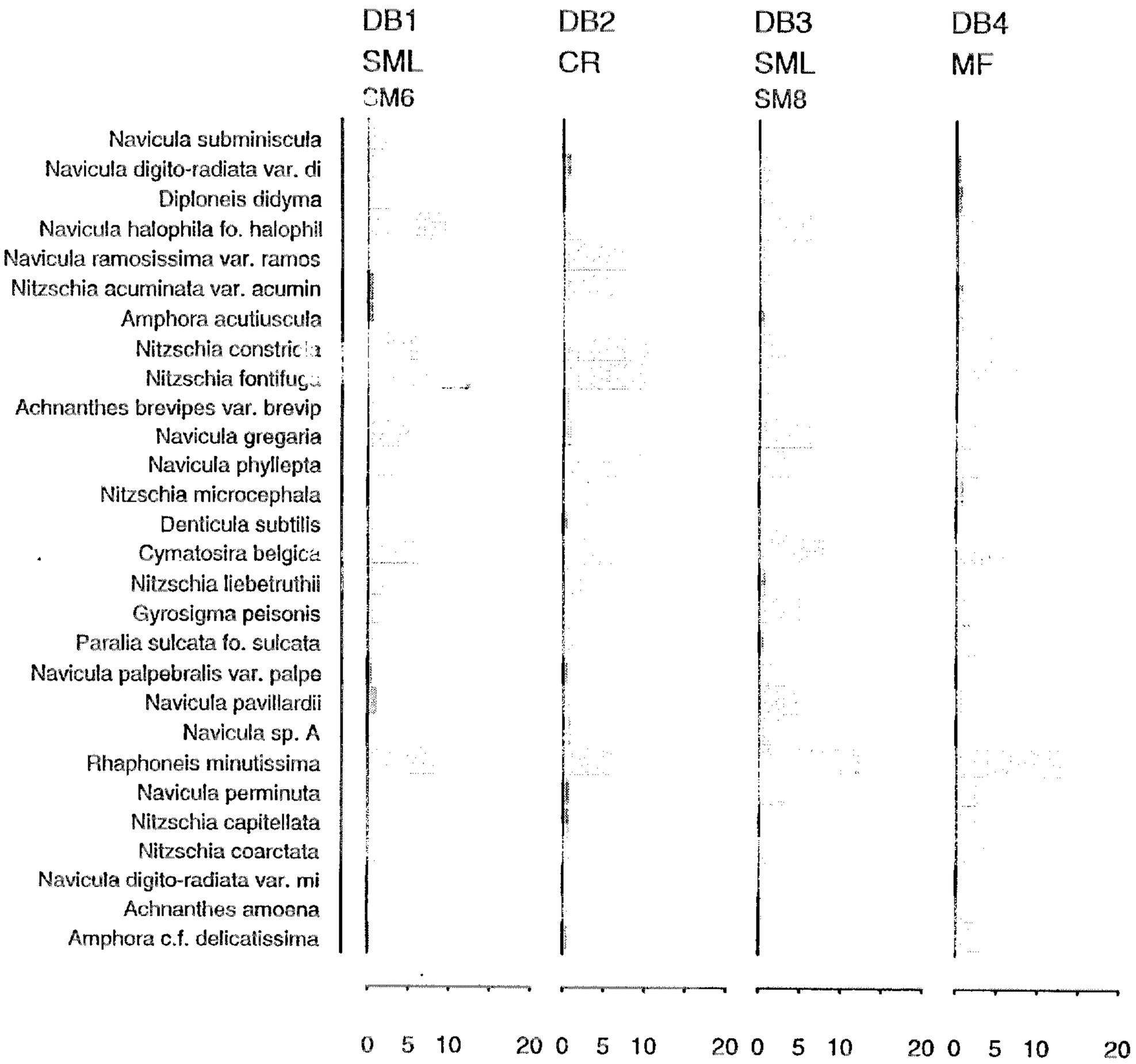
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Caerlaverock, Solway Firth



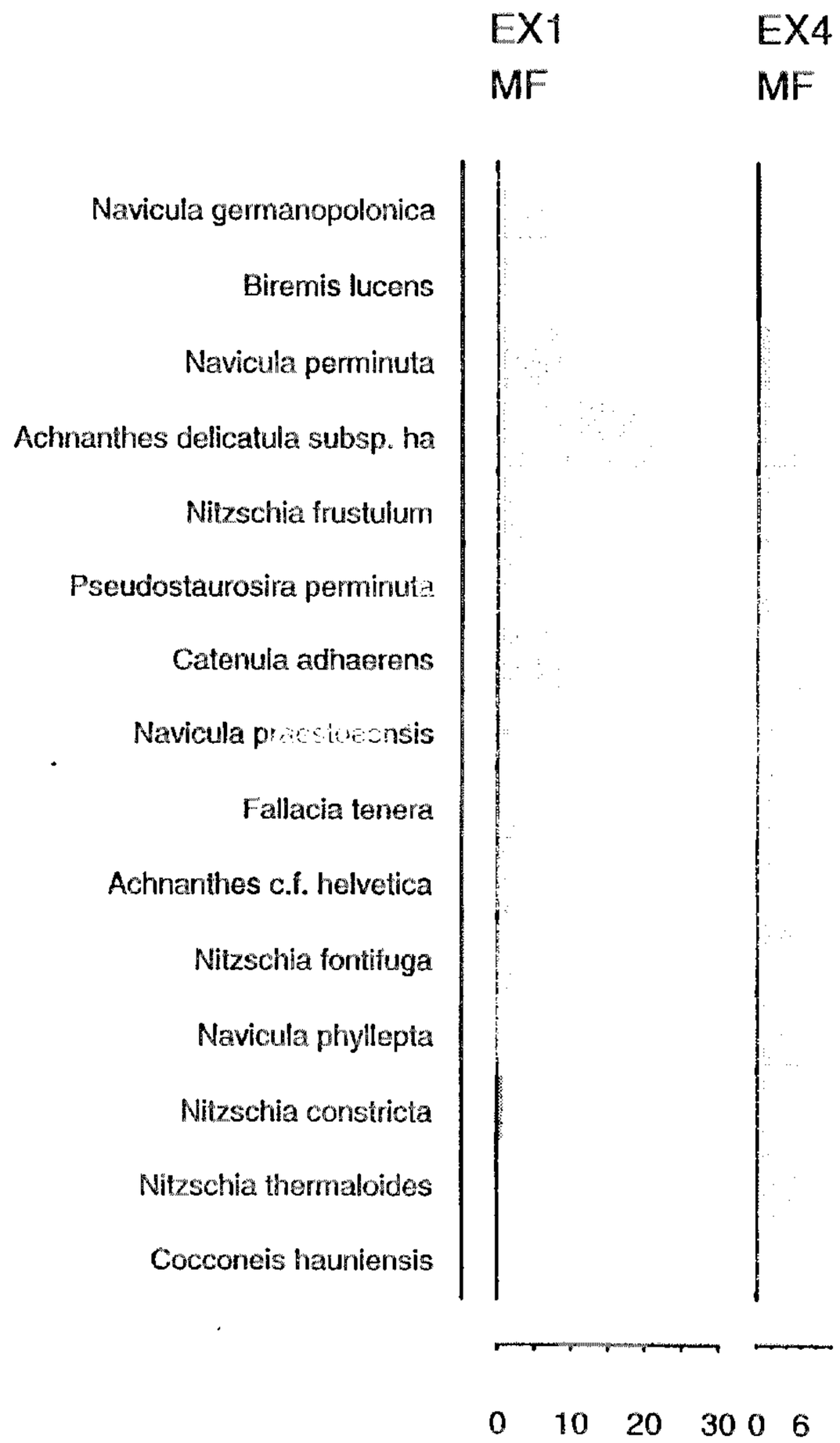
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Deben, South East Anglia



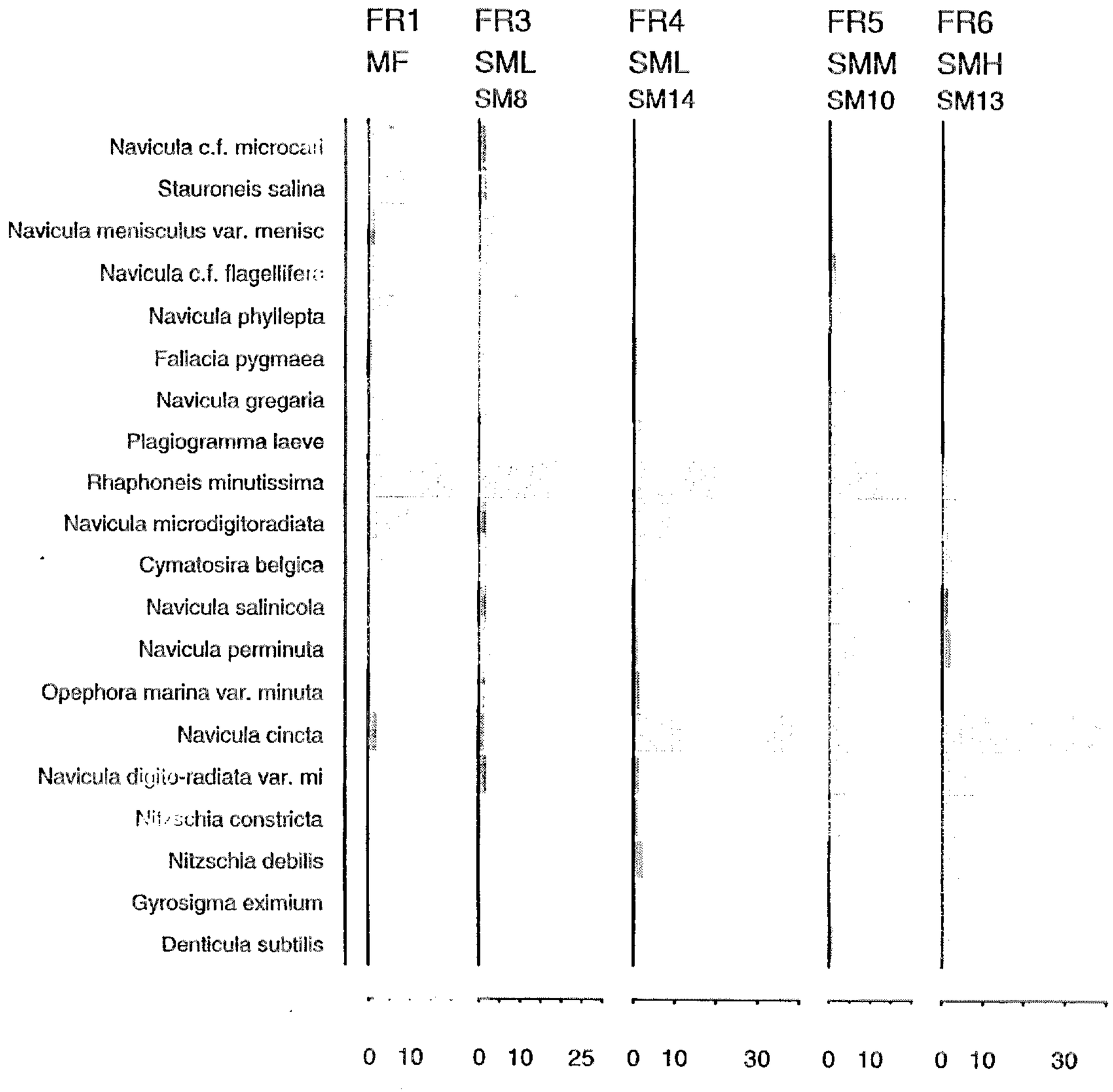
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Exe, South Coast



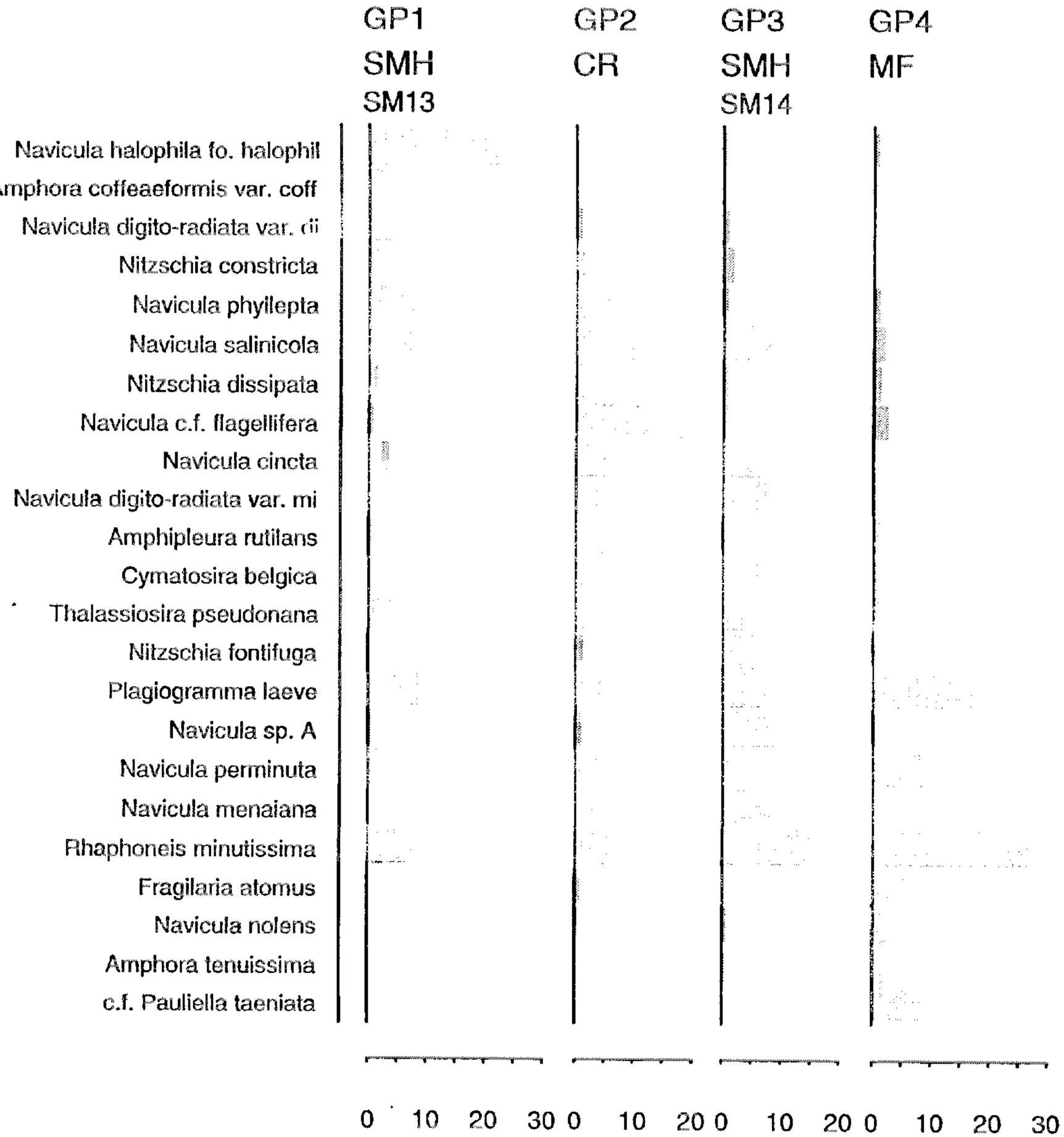
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Frampton, Wash



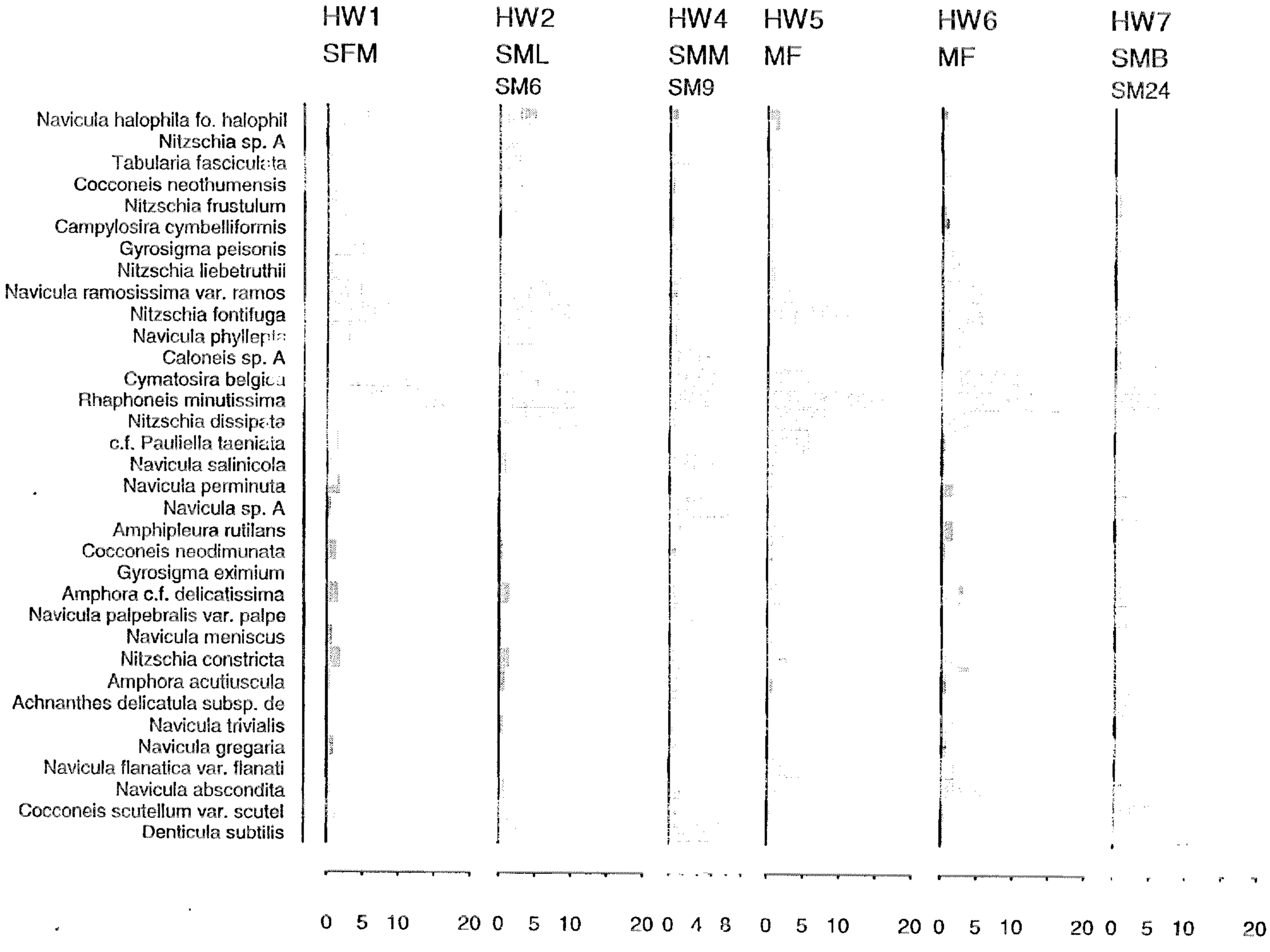
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Gibraltar Point, Wash



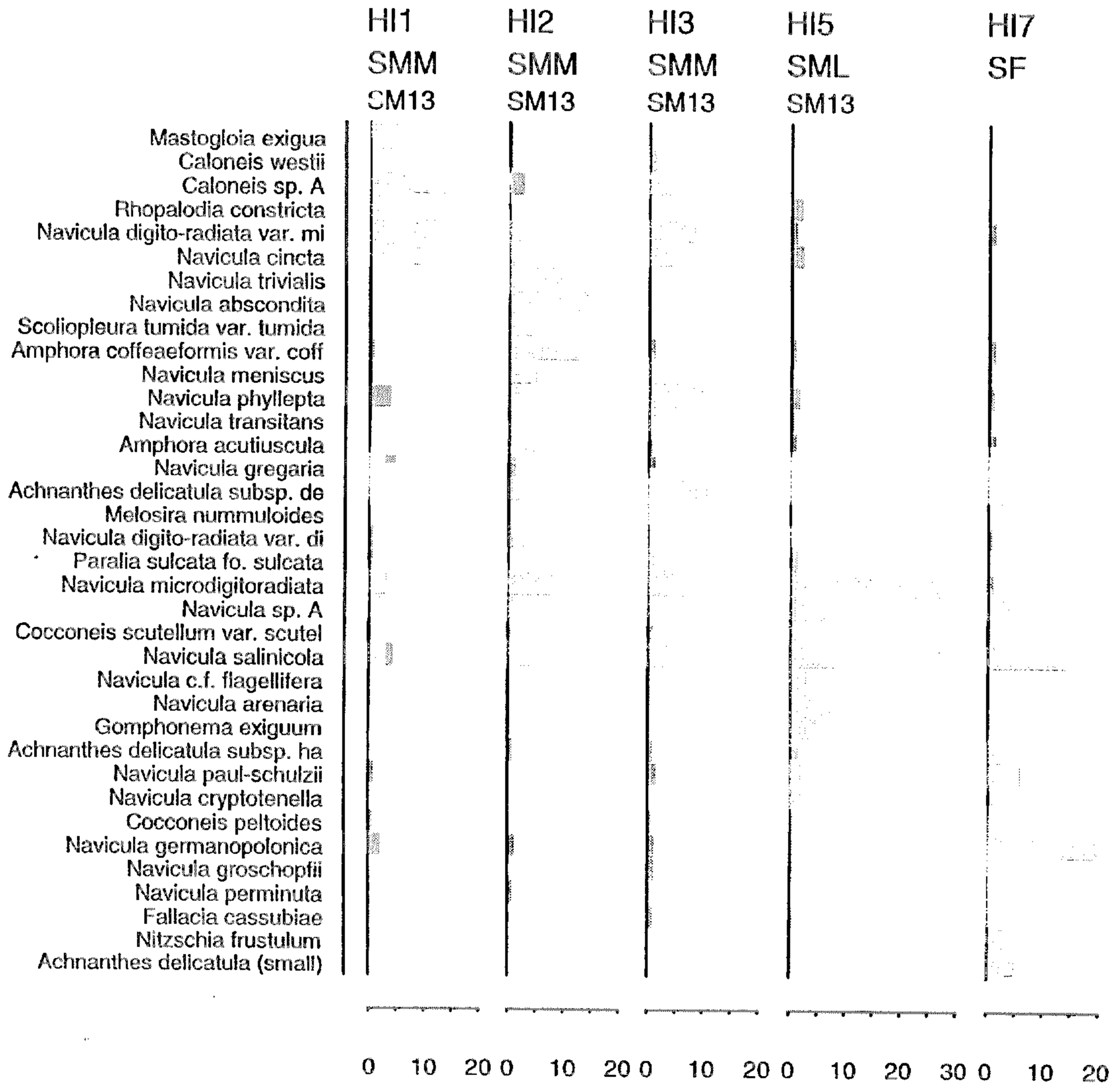
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Hamford Water, South East Anglia



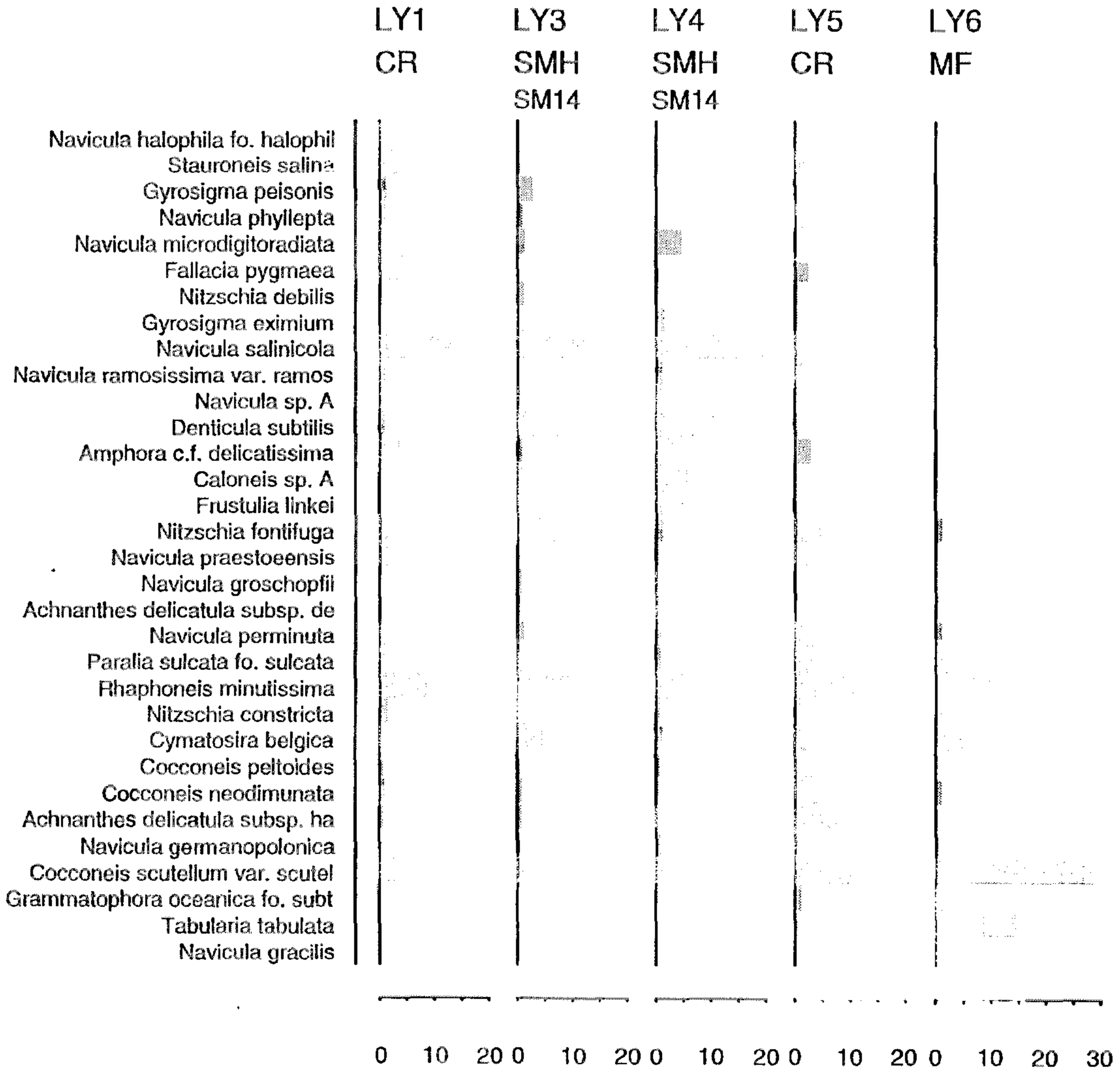
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Holy Island, North East



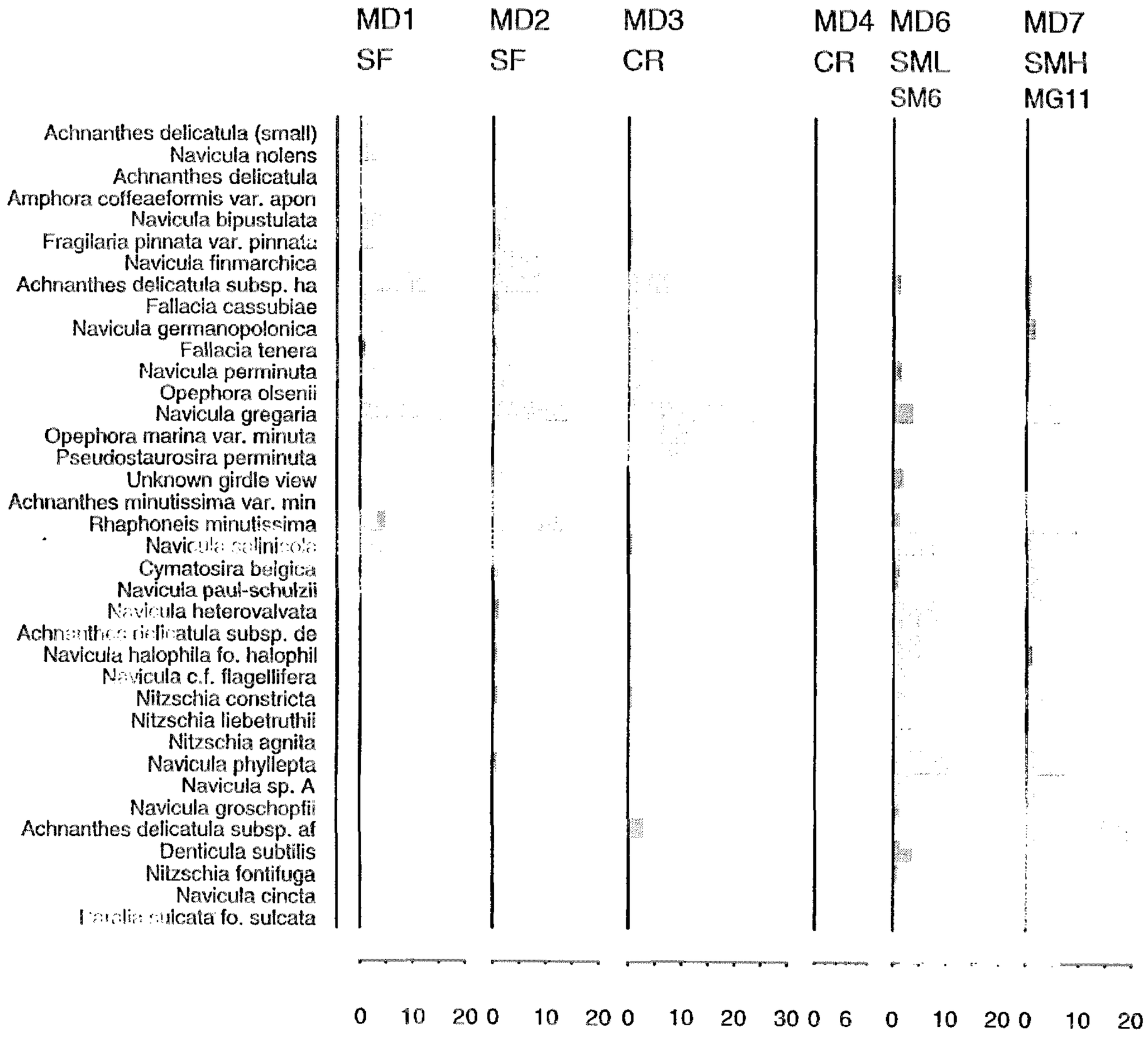
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Lymington, South Coast



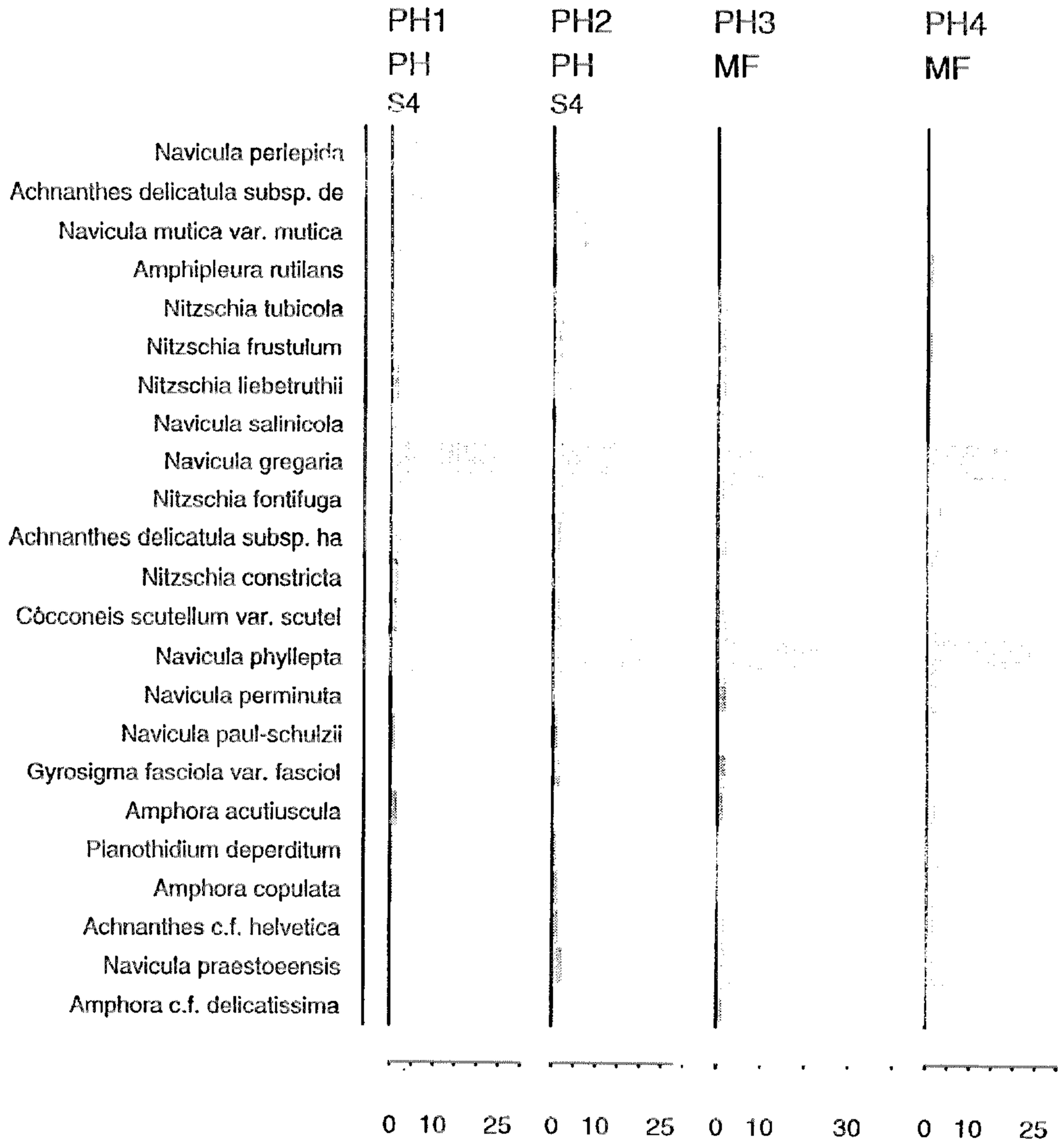
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Mawddach, Wales



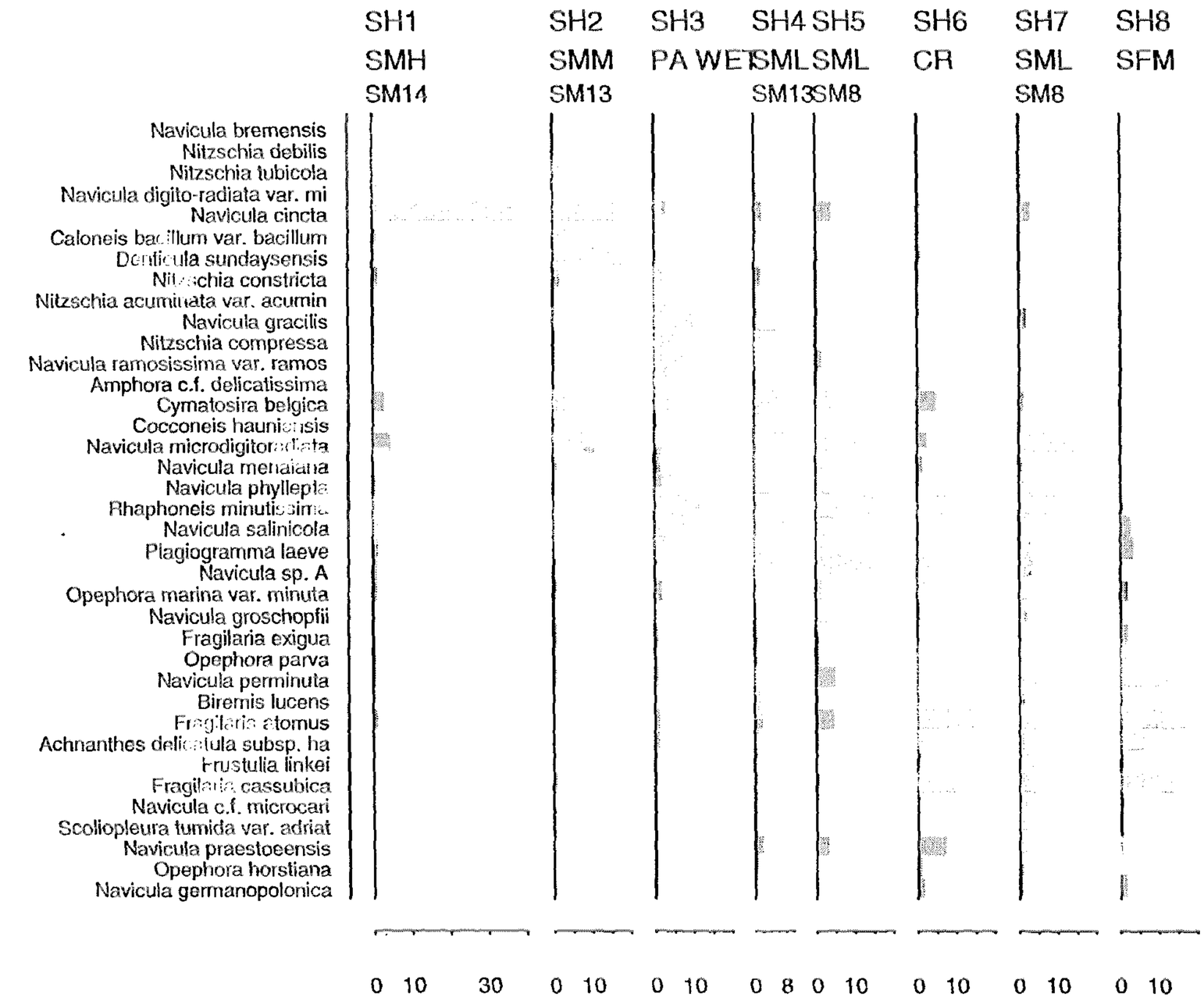
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Poole Harbour, South Coast



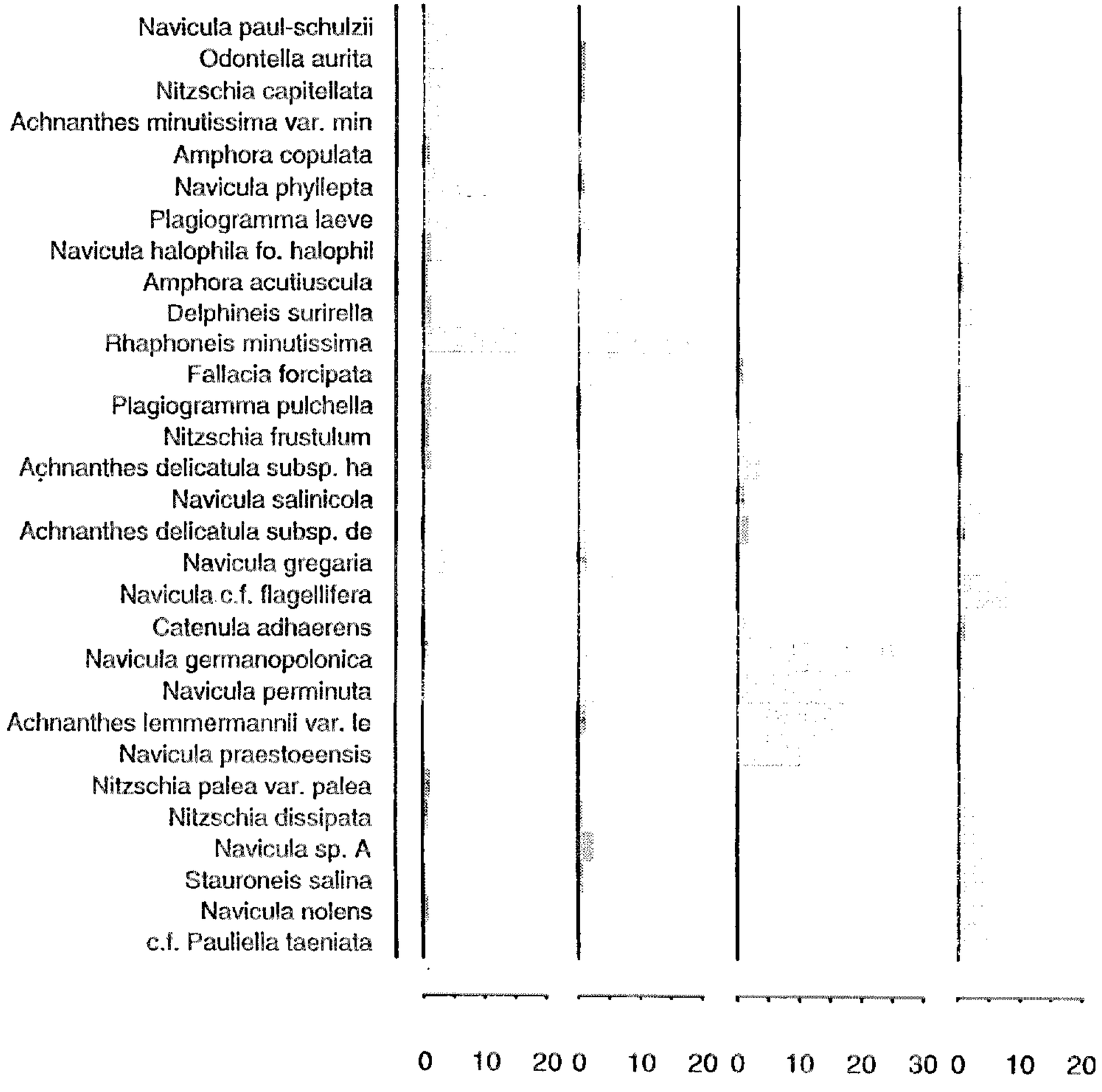
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Sailor's Home, Wash



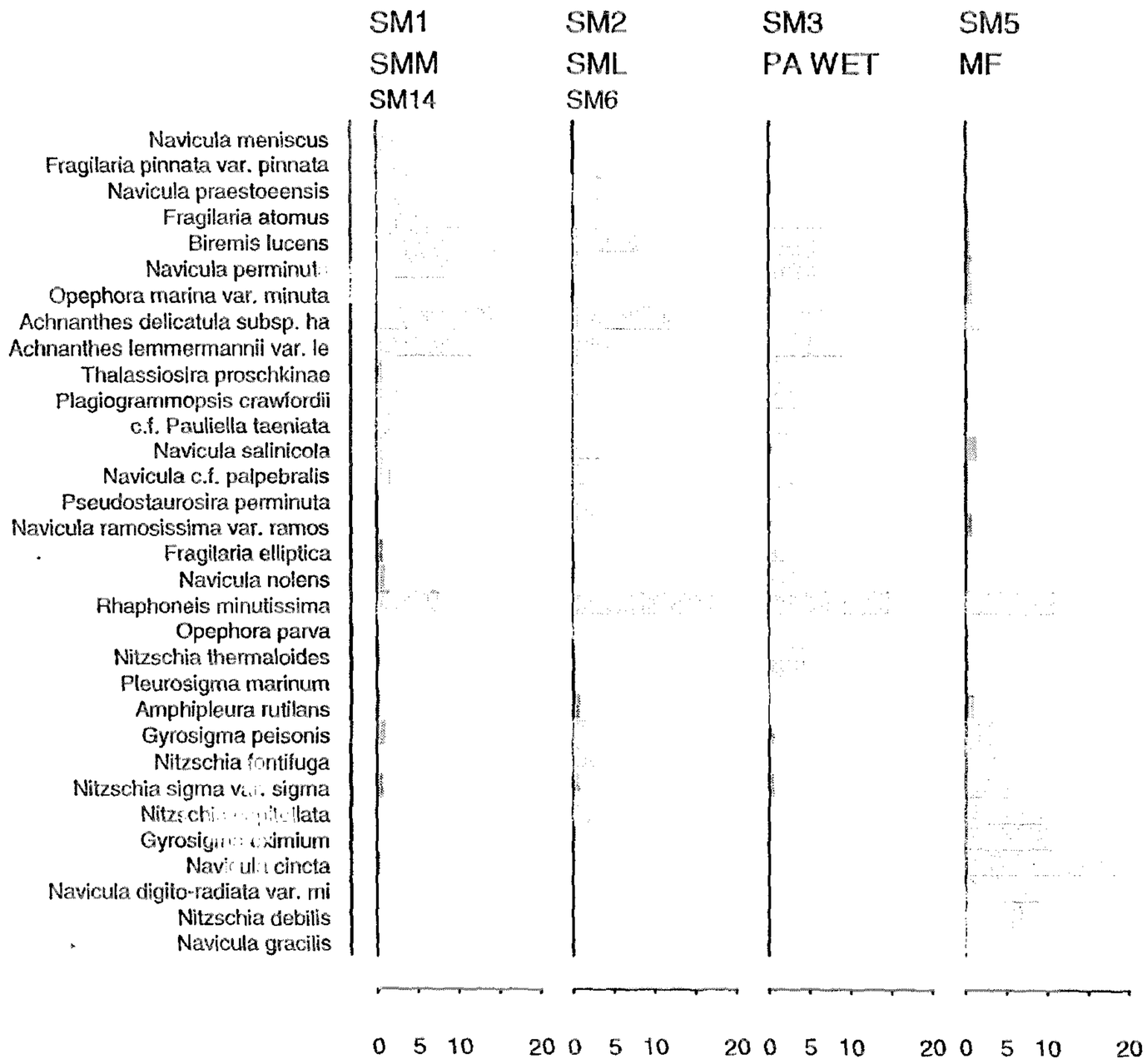
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Skyreburn Bay, Solway Firth



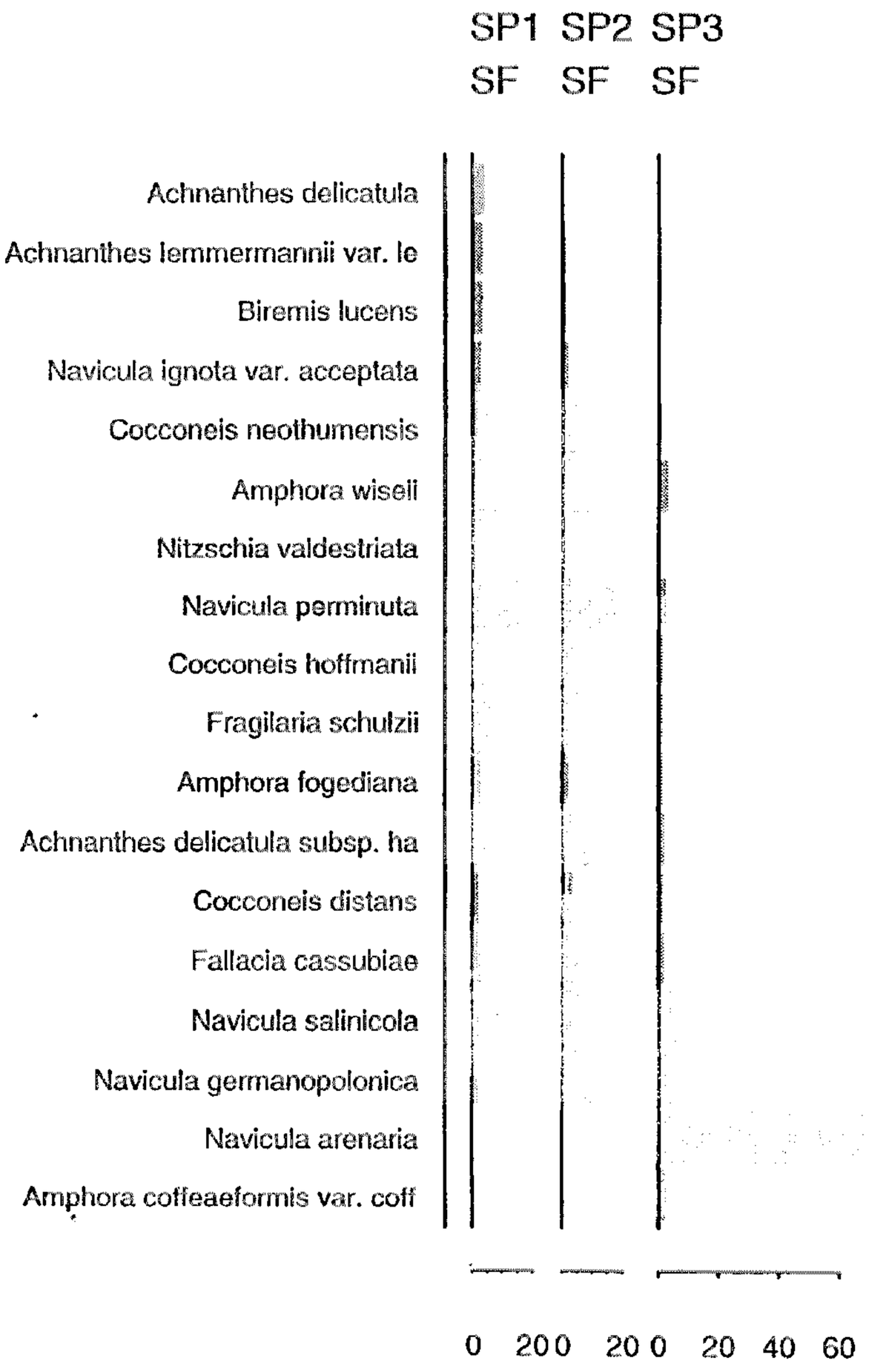
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Spurn Marsh, Humber



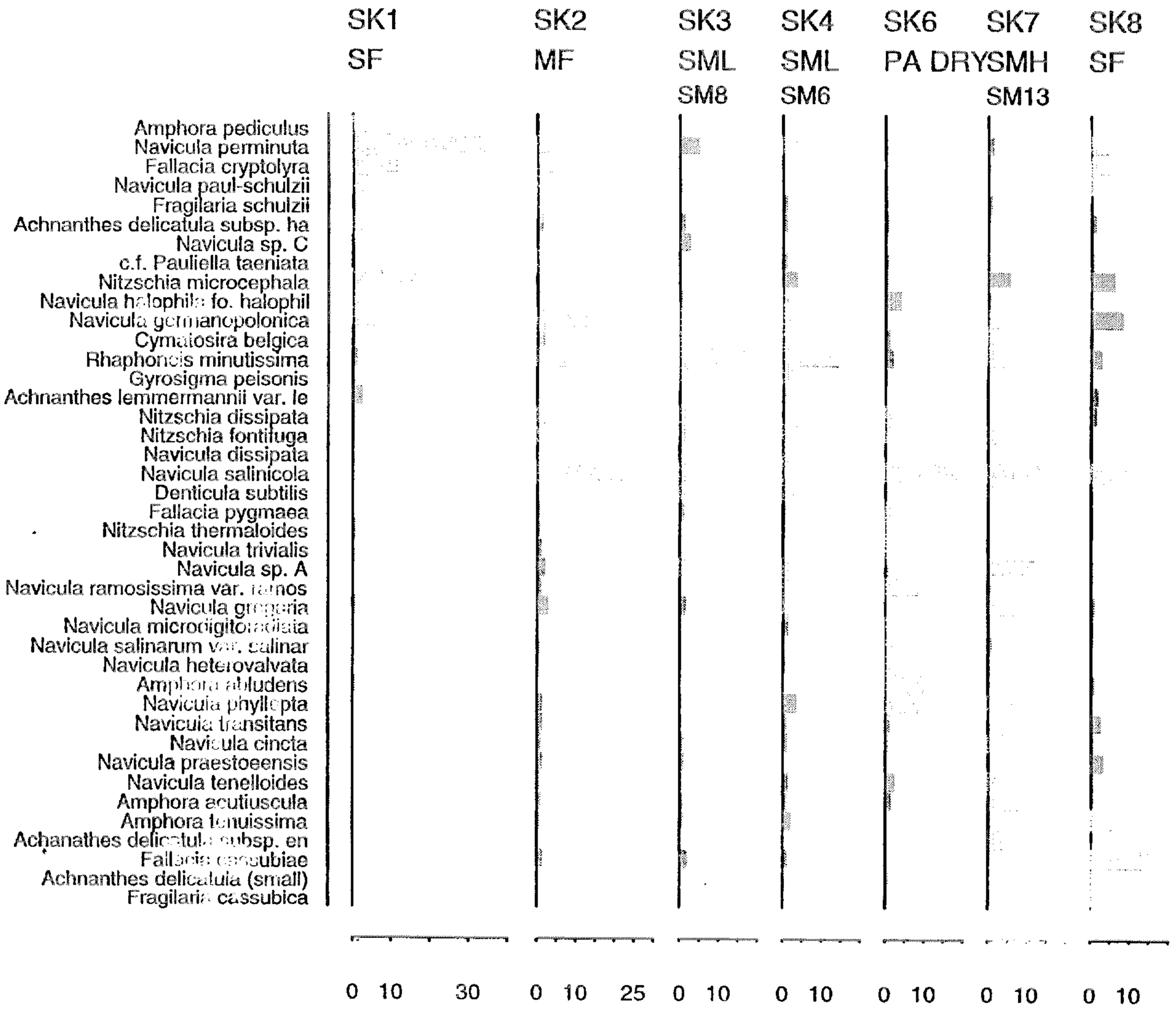
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Spurn Point, Humber



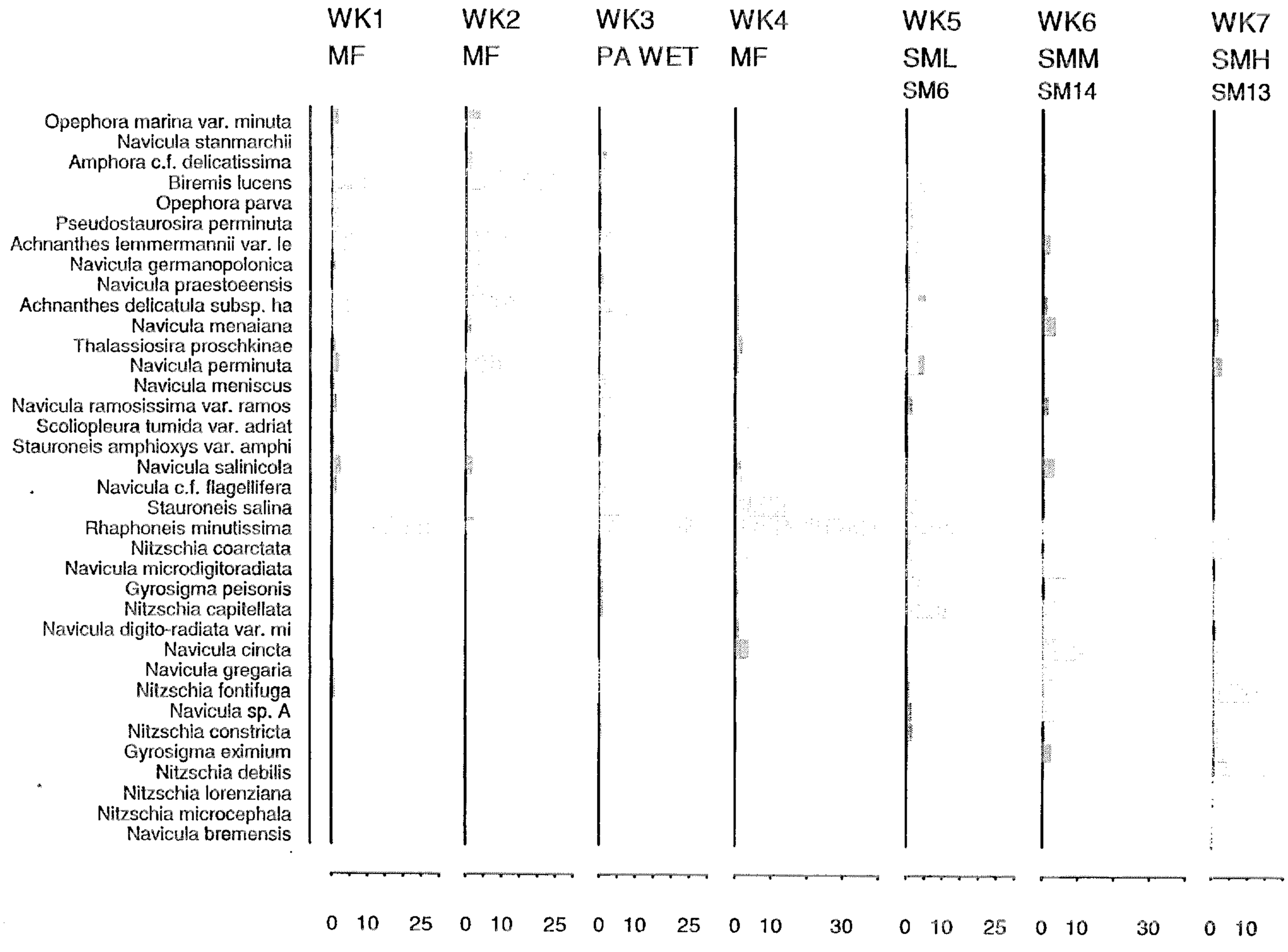
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Stiffkey, Norfolk



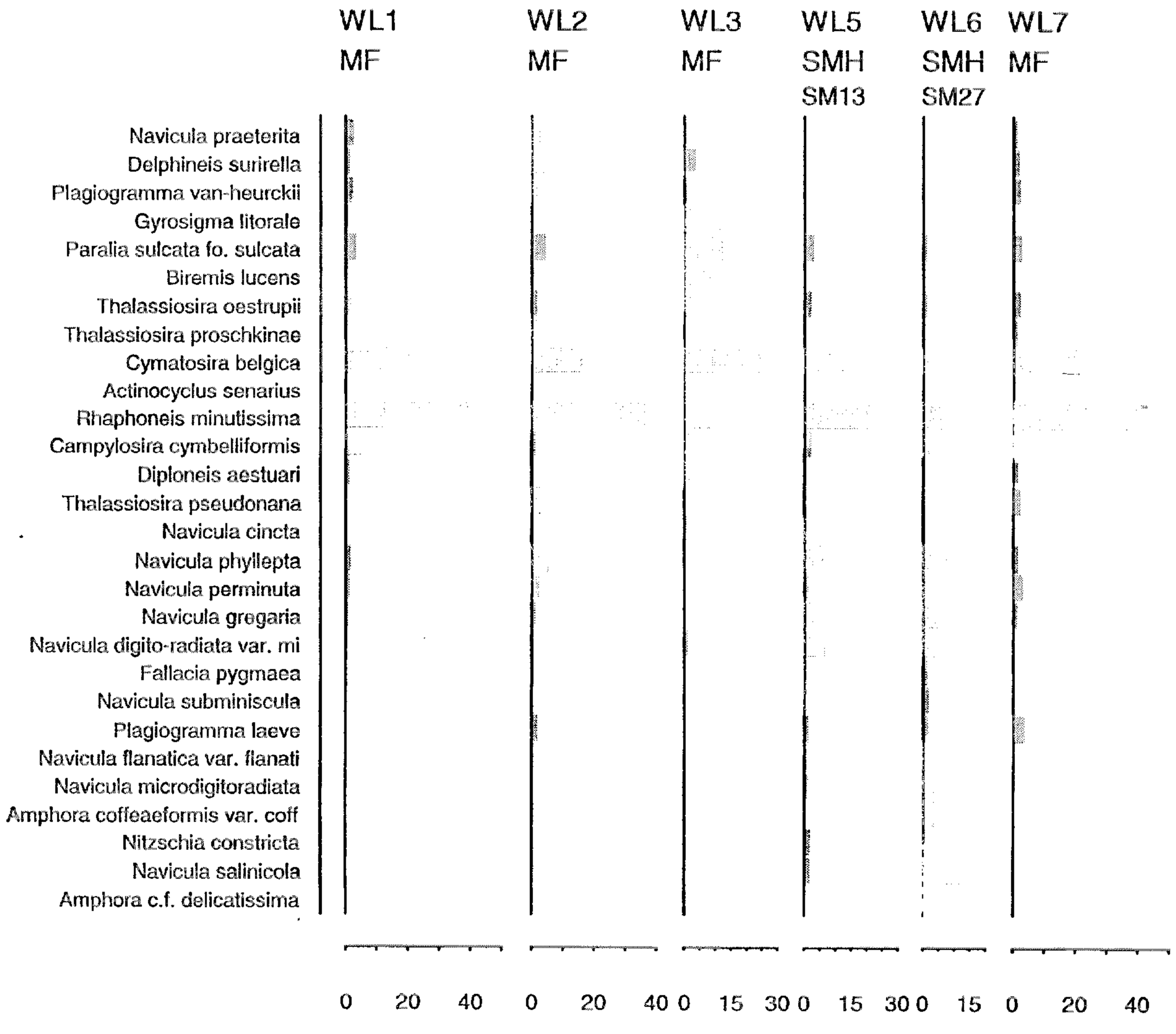
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Welwick, Humber



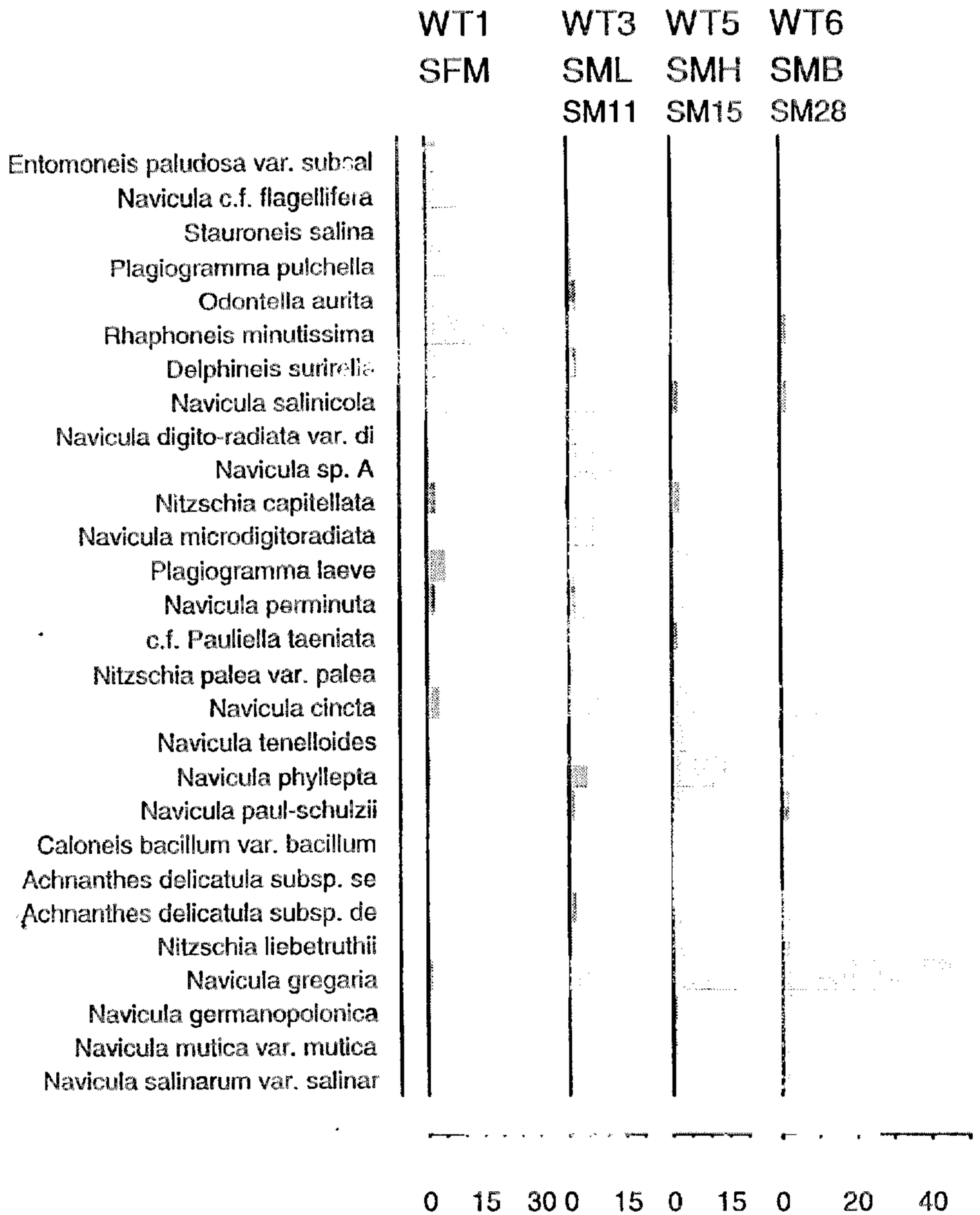
APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Wentlooge, Severn Estuary



APPENDIX 3
Distribution of diatom species across individual Sampling Sites

Wigtown, Solway Firth



APPENDIX 4

Average abundance of taxa within each habitat (for species with an abundance >2% in any one sample)

KEY: PH = Phragmites australis beds; SMB = back saltmarsh; SMH = high saltmarsh; SMM = mid saltmarsh; SML = low/pioneer saltmarsh; CR = creek; MF = mudflat; MFS = sandy mudflat; SF = sandflat

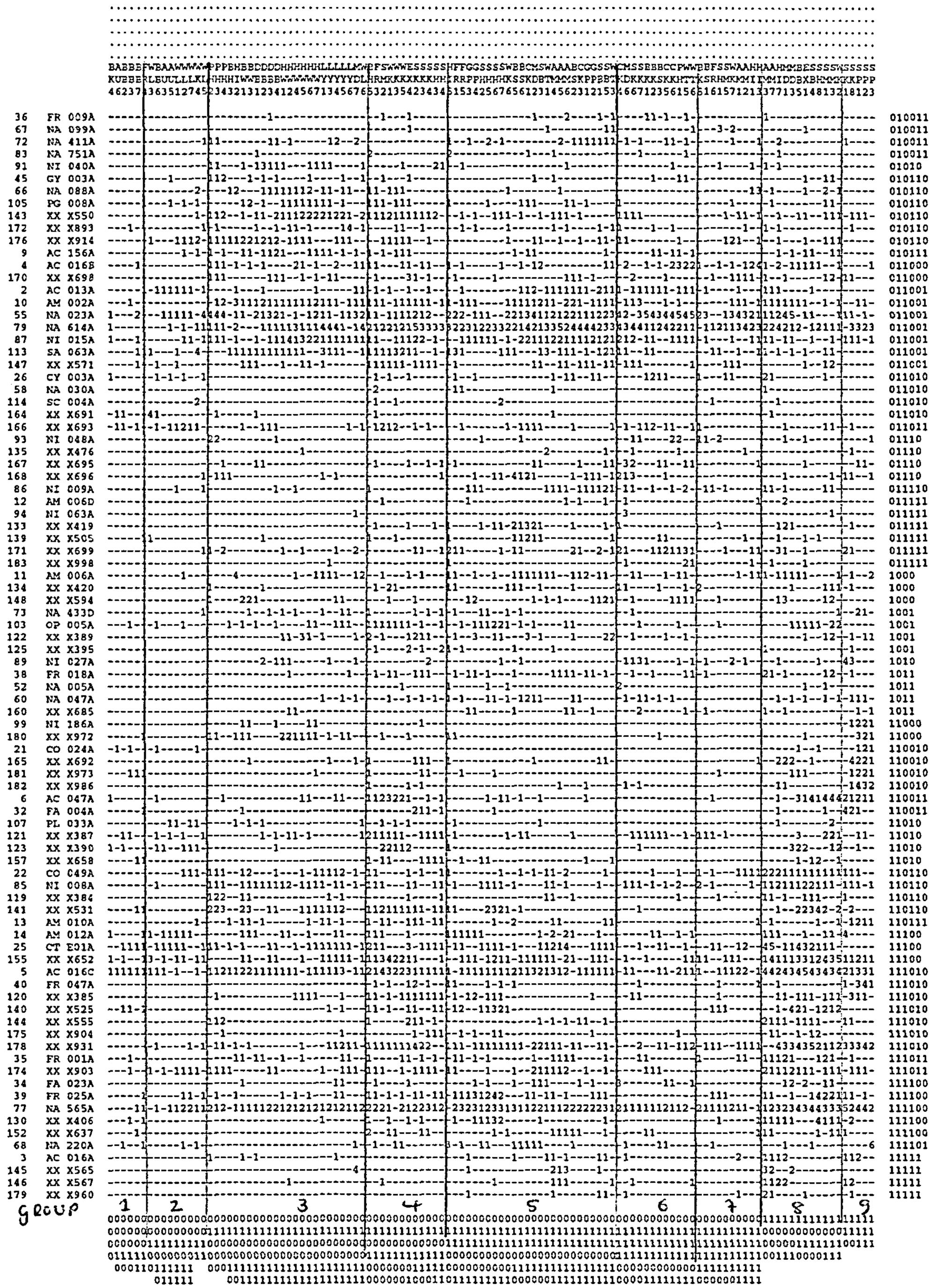
SPECIES	PH	SMB	SMH	SMM	SML	PAN WET	PAN DRY	CR	MF	MFS	SF
Achnanthes delicatula subsp. aff. engellbrechtii	0.00	0.00	1.02	0.00	0.17	0.00	0.00	1.10	0.28	0.56	0.00
Achnanthes delicatula subsp. delicatula	1.82	1.33	0.31	1.66	0.53	0.00	0.00	0.19	0.18	0.54	0.50
Achnanthes delicatula subsp. hauckiana	1.08	0.61	0.51	1.94	1.82	2.44	1.10	3.72	2.68	5.14	4.01
Achnanthes groenlandica	0.00	0.00	0.00	0.00	0.00	0.00	2.76	0.00	0.00	0.00	0.00
Achnanthes lanceolata	0.04	1.84	0.04	0.00	0.04	0.00	0.00	0.03	0.10	0.06	0.01
Achnanthes lemmermannii	0.16	0.00	0.10	1.25	0.46	2.97	0.00	0.22	0.75	0.23	1.76
Amphipleura rutilans	0.70	0.41	0.38	0.78	0.78	0.86	0.00	0.78	0.44	0.11	0.08
Amphora abludens	0.00	0.16	0.10	0.00	0.04	0.93	5.27	0.13	0.03	2.61	0.36
Amphora acutiuscula	0.29	0.44	0.57	0.87	0.35	0.53	0.62	0.62	0.57	0.94	0.34
Amphora coffeaeformis	0.04	0.08	0.50	1.26	0.12	0.12	0.41	0.21	0.08	0.40	0.51
Amphora copulata	0.28	0.00	0.08	0.09	0.09	0.31	0.40	0.05	0.24	1.47	0.20
Amphora pediculus	0.12	0.08	0.06	0.07	0.23	0.12	0.00	0.30	0.26	0.34	0.63
Amphora tenuissima	0.00	0.73	0.04	0.11	0.23	0.24	0.10	0.27	0.25	0.00	0.63
Amphora wiseii	0.00	0.00	0.02	0.00	0.06	0.00	0.00	0.00	0.04	0.00	1.55
Biremis lucens	0.17	0.12	0.12	1.40	0.77	2.37	0.00	0.89	2.24	2.12	0.98
c.f. Pauliella taeniata	0.00	1.63	0.08	0.13	0.36	0.48	0.21	0.10	0.48	0.23	0.73
Caloneis sp. A	0.00	0.12	0.81	2.86	0.32	0.00	0.20	0.00	0.04	0.00	0.01
Catenula adhaerens	0.16	0.04	0.14	0.44	0.46	0.28	0.59	2.21	1.19	3.50	1.26
Cocconeis neothumensis	0.20	0.20	0.02	0.07	0.18	0.00	0.00	0.05	0.21	0.60	0.56
Cocconeis scutellum	0.53	1.05	0.43	0.29	0.40	0.08	0.20	2.01	1.62	0.37	0.04
Cymatosira belgica	3.78	1.33	2.09	4.78	5.08	0.77	2.78	2.35	7.41	2.04	0.23
Delphineis surirella	0.49	0.16	0.58	0.70	0.76	0.55	0.59	0.15	0.84	2.12	0.43
Denticula subtilis	0.04	3.71	1.69	1.07	1.02	0.00	0.10	0.18	0.04	0.00	0.00
Denticula sundaysensis	1.95	0.48	0.40	1.73	0.04	0.16	0.00	0.22	0.00	0.03	0.01
Fallacia cassubiae	0.00	0.00	0.03	0.05	0.13	0.00	0.00	0.28	0.12	0.00	1.90
Fallacia cryptolyra	0.00	0.00	0.00	0.02	0.04	0.00	0.00	0.05	0.16	0.00	0.99
Fallacia forcipata	0.00	0.04	0.06	0.09	0.05	0.99	0.00	0.02	0.07	1.67	0.29
Fallacia pygmaea	0.08	0.16	0.56	0.22	0.47	1.84	1.24	0.84	0.12	0.00	0.09
Fallacia tenera	0.00	0.36	0.12	0.02	0.03	1.43	0.00	0.43	0.16	0.53	0.08
Fragilaria atomus	0.00	1.02	0.19	0.56	0.59	0.68	0.00	2.04	0.17	2.42	0.27
Fragilaria cassubica	0.00	0.04	0.01	0.11	0.23	0.24	0.00	1.58	0.15	2.02	0.25
Fragilaria schulzii	0.00	0.00	0.04	0.02	0.09	0.00	0.00	0.00	0.15	0.03	1.11
Gyrosigma eximium	0.61	0.24	1.06	0.71	1.08	0.04	0.00	0.08	0.40	0.06	0.00
Gyrosigma litorale	0.00	0.00	0.00	0.16	0.07	0.00	0.00	0.00	0.49	0.03	0.00
Gyrosigma peisonis	0.44	0.32	0.69	0.98	1.66	0.29	0.10	0.43	0.64	0.69	0.04
Mastogloia exigua	0.00	0.08	0.00	0.52	0.00	0.00	0.00	0.00	0.02	0.00	0.01
Navicula abscondita	0.20	0.24	0.04	1.45	0.09	1.25	0.00	0.10	0.46	0.06	0.09
Navicula arenaria	0.00	0.00	0.04	0.07	0.40	0.25	0.00	0.00	0.01	0.09	4.10
Navicula bipustulata	0.00	0.00	0.01	0.03	0.06	0.56	0.00	0.07	0.03	0.58	0.95
Navicula bremensis	0.00	0.04	0.62	0.00	0.01	0.00	0.00	0.00	0.01	0.03	0.02
Navicula c.f. flagellifera	0.26	0.45	0.23	0.27	0.76	0.46	0.00	2.64	0.97	2.73	0.50
Navicula c.f. microcari	0.00	0.04	0.21	0.00	0.39	0.08	0.00	0.08	0.21	0.42	0.18
Navicula cincta	16.66	2.46	9.53	10.82	3.38	0.97	1.19	0.89	1.00	1.03	0.07

Appendix 4 continued

SPECIES	PH	SMB	SMH	SMM	SML	PAN WET	PAN DRY	CR	MF	MFS	SF
Navicula digito-radiata var. minima	2.46	0.00	2.30	3.31	0.36	0.08	1.39	0.53	0.42	0.62	0.10
Navicula finmarchica	0.00	0.00	0.04	0.00	0.02	0.00	0.00	0.03	0.01	0.14	0.68
Navicula flanatica	0.13	0.20	0.29	0.04	0.26	0.69	0.00	0.20	1.10	0.62	0.13
Navicula germanopolonica	0.21	0.89	0.46	0.55	0.39	0.33	0.00	1.21	0.98	1.28	5.81
Navicula gracilis	0.00	0.00	0.00	0.66	0.11	2.02	0.00	0.00	0.37	0.00	0.05
Navicula gregaria	9.60	12.33	4.93	2.11	1.57	3.18	0.00	4.12	3.58	1.11	2.64
Navicula halophila	0.12	0.28	1.39	0.16	1.51	1.59	1.87	0.55	0.35	1.03	0.29
Navicula heterovalvata	0.00	0.36	0.09	0.07	0.54	0.00	2.39	0.10	0.11	0.25	0.17
Navicula lucinensis	0.00	1.08	0.23	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Navicula menaiana	0.05	0.61	0.50	0.52	0.55	2.23	0.10	0.52	0.44	0.21	0.13
Navicula meniscus	0.00	0.00	0.01	1.16	0.08	0.25	0.98	0.15	0.34	0.17	0.00
Navicula microdigitoradiata	0.08	0.12	1.64	4.53	4.14	1.17	4.78	1.00	0.61	0.76	0.12
Navicula mutica	4.84	1.93	0.53	0.23	0.14	0.00	0.20	0.03	0.04	0.00	0.01
Navicula nolens	0.36	0.69	0.09	0.07	0.06	0.60	0.10	0.05	0.22	0.15	0.70
Navicula paul-schulzii	0.33	0.36	0.76	0.27	0.26	1.38	0.00	0.00	0.34	0.32	0.79
Navicula perlepida	1.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Navicula perminuta	1.58	2.19	1.38	1.70	2.46	2.59	0.10	3.21	2.23	4.93	7.18
Navicula phyllepta	8.38	1.82	3.20	1.75	2.55	4.48	4.15	3.55	4.90	0.75	0.33
Navicula praestoeensis	0.44	0.16	0.03	0.37	0.61	0.21	0.00	1.31	1.10	2.62	0.94
Navicula ramosissima	0.00	0.04	0.12	0.23	1.04	2.04	4.46	1.36	0.61	0.72	0.00
Navicula salinarum	0.28	0.73	0.04	0.00	0.04	0.12	2.80	0.00	0.02	0.00	0.04
Navicula salinicola	0.73	1.37	5.90	3.72	4.84	7.91	9.02	4.72	1.98	4.14	4.35
Navicula sp. A	0.16	1.08	2.79	2.88	3.81	1.06	0.21	0.86	0.11	1.97	0.69
Navicula trivialis	0.04	0.04	0.02	0.89	0.23	0.04	1.76	0.17	0.21	0.00	0.00
Nitzschia acuminata	0.04	0.08	0.07	0.04	0.17	0.77	0.00	0.85	0.13	0.09	0.01
Nitzschia agnita	0.00	0.00	0.07	0.00	0.26	0.12	0.00	0.00	0.00	0.00	0.00
Nitzschia capitellata	0.16	0.44	0.70	0.61	0.93	0.17	0.00	0.10	0.72	0.55	0.02
Nitzschia clausii	2.83	0.84	0.57	0.18	0.02	0.04	0.31	0.00	0.02	0.00	0.02
Nitzschia compressa	0.12	0.04	0.03	0.04	0.30	1.09	0.41	0.13	0.17	0.06	0.00
Nitzschia constricta	1.18	0.89	1.69	1.70	0.90	1.30	10.65	1.81	1.15	0.37	0.07
Nitzschia debilis	2.47	1.16	2.02	0.09	0.09	0.04	0.00	0.05	0.27	0.00	0.00
Nitzschia dissipata	0.69	0.85	0.44	0.29	1.05	0.89	1.35	0.86	0.88	0.55	0.84
Nitzschia fontifuga	1.18	0.64	2.16	0.50	1.77	1.04	0.73	2.20	2.33	1.72	0.09
Nitzschia microcephala	0.04	0.32	0.46	0.05	0.32	0.00	0.10	0.38	0.04	0.20	1.30
Nitzschia navicularis	0.00	0.00	0.09	0.18	0.04	0.04	6.50	0.03	0.02	0.00	0.00
Nitzschia sigma	1.85	0.36	0.49	0.89	0.27	0.37	0.20	0.30	1.07	0.17	0.01
Nitzschia thermaloides	0.20	0.20	0.19	0.14	0.03	0.85	1.14	0.08	0.28	0.08	0.13
Odontella aurita	0.21	0.04	0.13	0.20	0.34	0.50	0.00	0.12	0.39	1.10	0.12
Opephora marina var. minuta	0.00	0.00	0.05	0.47	0.33	0.36	0.00	2.86	0.36	0.20	0.14
Paralia sulcata	0.77	0.12	0.73	1.99	0.92	0.29	1.18	1.26	1.69	0.69	0.05
Plagiogramma laeve	0.58	3.46	1.36	0.57	1.07	0.73	0.00	1.07	0.87	1.32	0.29
Plagiogramma pulchella	0.00	0.16	0.20	0.00	0.10	0.82	0.00	0.13	0.19	1.29	1.17
Plagiogramma van-heurckii	0.37	0.20	0.27	0.27	0.42	0.73	0.00	0.18	0.80	0.76	1.07
Plagiogrammopsis crawfordii	0.05	0.00	0.13	0.32	0.25	1.01	0.10	0.03	0.30	0.00	0.59
Pseudostaurosira perminuta	0.04	0.00	0.01	0.02	0.18	0.32	0.00	1.15	0.42	0.00	0.23
Rhaphoneis minutissima	9.37	6.95	7.97	8.87	11.82	13.32	2.01	5.52	17.91	12.85	4.01
Rhopalodia constricta	0.00	0.00	0.00	0.52	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Stauroneis salina	0.04	0.00	0.13	0.51	0.46	1.57	0.39	1.03	1.12	1.42	0.22
Tabularia tabulata	0.00	0.12	0.02	0.07	0.12	0.13	0.00	0.05	0.61	0.00	0.02
Thalassiosira oestrupii	0.25	0.00	0.17	0.58	0.47	0.04	0.00	0.05	0.87	0.06	0.12
Thalassiosira pseudonana	0.04	1.22	0.52	0.05	0.07	0.04	0.00	0.18	0.40	0.09	0.06

APPENDIX 5

TWINSPAN Two-way table



KEY to TWINSPAN two-way table: Plot values indicate the following weighted abundance cut-off levels: 1 = 0-<2; 2 = >2-,5; 3 = >5-<10; 4 = >10-<20; 5 = >20-<50;6 = >50.

APPENDIX 6

Significance tests for diatom species distributions over the normalised tidal gradient (For species with an average abundance >5% in any one sample)

Species Name	Species code	Distribution Model with best fit to tidal gradient	Maximum percentage abundance	Number of samples containing taxon	N_2 diversity
Achnanthes delicatula subsp. aff. *engelbrechtii*	XXX565	GAM	18.9	9	3.93
Achnanthes delicatula subsp. *hauckiana*	AC016C	GAM	21.1	100	33.23
Achnanthes lanceolata	AC001A	GAM	8.6	22	2.76
Achnanthes lemmermannii	AC047A	GAM	15.2	36	11.5
Amphipleura rutilans	AP002A	GAM	8.7	52	19.38
Amphora abludens	XXX696	GAM	18.3	28	4.39
Amphora copulata	XXX653	GAM	6.3	34	11.52
Amphora pediculus	AM012A	GAM	10.3	42	7.41
Amphora wiseii	XXX986	GAM	13.3	13	3.13
Biremis lucens	XXX652	GAM	28.9	73	13.42
c.f. *Pauliella taeniata*	XXX389	GAM	8.1	30	11.59
Caloneis sp. A	XXX538	GAM	16.6	22	6.87
Catenula adhaerens	CTE01A	GAM	21.1	67	10.87
Cocconeis scutellum	CO007A	GAM	28.5	53	8.08
Cymatosira belgica	CT001A	GAM	30.5	77	34.11
Denticula subtilis	XXX649	GAM	18.5	36	10.7
Denticula sundaysensis	XXX399	GAM	19.0	15	3.67
Fallacia cassubiae	XXX692	GAM	14.3	20	6.35
Fallacia cryptolyra	FA004A	GAM	11.1	12	3.27
Fallacia tenera	FA023A	GAM	6.9	22	8.11
Fragilaria atomus	FR025A	GAM	16.2	49	9.32
Fragilaria cassubica	XXX406	GAM	13.2	27	5.94
Fragilaria schulzii	FR047A	GAM	10.8	18	3.93
Gyrosigma eximium	GY014A	GAM	20.8	35	6.9
Gyrosigma litorale	XXX691	GAM	11.2	9	2.1
Mastogloia exigua	MA014A	GAM	5.5	6	1.56
Navicula arenaria	NA220A	GAM	67.6	25	1.45
Navicula bremensis	NA099A	GAM	8.7	8	2.03
Navicula c.f. *flagellifera*	XXX396	GAM	18.5	64	17.56
Navicula c.f. *microcari*	XXX618	GAM	5.8	21	7.57
Navicula cincta	NA021A	GAM	61.2	76	18
Navicula digito-radiata var. minima	XXX688	GAM	13.2	50	19.83
Navicula finmarchica	NA359A	GAM	8.2	14	2.64
Navicula flanatica	NA363B	GAM	8.9	50	14.1
Navicula germanopolonica	XXX931	GAM	24.8	71	17.35

Appendix 6 continued

Species Name	Species code	Model with best fit to tidal gradient data	Maximum percentage abundance	Number of samples containing taxon	N2 diversity
Navicula gracilis	NA029A	GAM	10.1	15	4.73
Navicula gregaria	NA023A	GAM	44.4	89	28.64
Navicula lucinensis	NA748A	GAM	5.4	4	2.46
Navicula menaiana	NA509A	GAM	8.3	44	15.15
Navicula meniscus	NA088A	GAM	5.4	28	10.56
Navicula microdigitoradiata	XXX928	GAM	26.8	61	23.1
Navicula mutica var. *mutica*	NA025A	GAM	11.2	36	9.79
Navicula nolens	XXX594	GAM	7.2	27	9.81
Navicula perminuta	NA565A	GAM	34.0	105	39.05
Navicula phyllepta	NA058A	GAM	30.8	88	33.69
Navicula praestoeensis	XXX531	GAM	18.4	43	13.92
Navicula ramosissima	NA059A	GAM	8.9	38	16.91
Navicula salinicola	NA614A	GAM	27.0	98	46.33
Navicula sp. A	XXX643	GAM	16.0	61	26.89
Navicula trivialis	NA063A	GAM	9.0	20	6.11
Nitzschia agnita	NI063A	GAM	5.4	3	1.72
Nitzschia capitellata	NI028A	GAM	11.0	56	15.58
Nitzschia compressa	NI200A	GAM	5.5	20	6.4
Nitzschia debilis	NI088A	GAM	13.9	25	8.18
Nitzschia dissipata	NI015A	GAM	10.5	78	29.43
Nitzschia fontifuga	XXX391	GAM	12.3	76	31.2
Nitzschia microcephala	NI027A	GAM	15.8	22	5.94
Nitzschia navicularis	NI022A	GAM	13.0	18	1.99
Nitzschia sigma	NI006A	GAM	8.0	66	22.42
Opephora marina var. *minuta*	XXX525	GAM	16.4	30	7.54
Plagiogramma pulchella	XXX398	GAM	13.6	29	7.65
Plagiogramma van-heurckii	PR011A	GAM	17.2	66	12.92
Pseudostaurosira perminuta	XXX390	GAM	9.2	21	7.14
Rhaphoneis minutissima	RA007A	GAM	44.0	112	63.97
Rhopalodia constricta	XXX896	GAM	5.7	2	1.57
Stauroneis salina	SA063A	GAM	13.6	60	14.43
Tabularia tabulata	XXX893	GAM	14.8	28	2.22
Thalassiosira oestrupii	TH026A	GAM	5.3	43	17.07
Amphora tenuissima	XXX385	L	5.2	37	17.34
Cocconeis neothumensis	XXX972	L	5.5	24	9
Fallacia pygmaea	FA001A	L	6.9	47	17.02
Navicula abscondita	XXX401	L	14.3	27	6.36

Appendix 6 continued

Species Name	Species code	Model with best fit to tidal gradient data	Maximum percentage abundance	Number of samples containing taxon	N2 diversity
Navicula halophila	NA022A	L	22.2	50	12.52
Navicula salinarum	NA035A	L	5.6	15	4.72
Nitzschia constricta	NI083A	L	20.5	77	26.44
Plagiogramma laeve	PR005A	L	16.7	70	23.81
Achnanthes delicatula subsp. *delicatula*	AC016B	NS	10.3	49	18.27
Achnanthes groenlandica	AC074A	NS	5.5	1	1
Amphora acutiuscula	AM002A	NS	7.5	71	28.13
Amphora coffeaeformis var. *coffeaeformis*	AM006A	NS	12.3	45	9.69
Gyrosigma peisonis	GY021A	NS	8.2	66	30.43
Navicula bipustulata	XXX419	NS	8.0	20	6.82
Navicula heterovalvata	XXX695	NS	8.3	23	7.53
Navicula paul-schulzii	XXX699	NS	5.5	37	18.94
Navicula perlepida	NA564A	NS	7.4	1	1
Nitzschia acuminata var. *acuminata*	NI040A	NS	5.9	23	7.29
Nitzschia clausii	NI080A	NS	11.9	25	5.16
Nitzschia thermaloides	XXX698	NS	5.1	33	10.8
Odontella aurita	OD001A	NS	5.7	57	20.85
Paralia sulcata	PA001A	NS	12.4	83	33.51
Plagiogrammopsis crawfordii	XXX387	NS	7.5	44	13.08
Thalassiosira pseudonana	TH031A	NS	5.9	25	11.6
Delphineis surirella	DEL01A	Q	7.3	74	33.78
Fallacia forcipata	FA007A	Q	5.5	27	10.02

APPENDIX 7

Sample Details

Sample	Estuary	Date	Site type	Tidal regime	Habitat	WWT community	Salinity (ppt)	Salinity categories	% Clay	% Silt	% Sand	Weight (g/0.01)	Weight of SM (g/0.01)	Weight relative to MI	Normalised total weight
AM1	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	SMH	SM13	13.5	Mesohaline	6.44	70.16	23.4	5.00	3.12	1.88	1.00
AM2	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	SMM	SM14	12.9	Mesohaline	5.78	69.02	25.2	4.93	3.12	1.81	0.96
AM3	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	CR		16.6	Mesohaline	7.07	75.33	17.6	5.00	3.12	1.88	1.00
AM4	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	SML	SM8	16.7	Mesohaline	5.91	72.59	21.5	4.50	3.12	1.38	0.73
AM5	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	SML	SM6	17.0	Mesohaline	7.21	82.59	10.2	4.51	3.12	1.39	0.74
AM6	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	MF		19.7	Polyhaline	4.96	62.74	32.3	4.20	3.12	1.08	0.57
AM7	Alnmouth	16-Dec-97	Bar-Built	Mesotidal	SFM		12.2	Mesohaline	2.37	25.13	72.5	4.00	3.12	0.88	0.47
BW1	Blackwater	13-Aug-98	Coastal Plain	Macrotidal	MF		26.0	Polyhaline	10.7	80.3	9	3.69	2.68	1.01	0.39
BW3	Blackwater	13-Aug-98	Coastal Plain	Macrotidal	MF		31.6	Euhaline	11.2	80.2	8.6	4.00	2.68	1.32	0.50
DB1	Debden	15-Aug-98	Coastal Plain	Mesotidal	SML	SM6	29.5	Polyhaline	9.39	74.71	15.9	3.10	2.00	1.10	0.55
DB2	Debden	15-Aug-98	Coastal Plain	Mesotidal	CR		32.5	Euhaline	8.43	67.87	23.7	2.89	2.00	0.89	0.44
DB3	Debden	15-Aug-98	Coastal Plain	Mesotidal	SML	SM8	24.5	Polyhaline	9.17	72.83	18	3.11	2.00	1.11	0.55
DB4	Debden	15-Aug-98	Coastal Plain	Mesotidal	MF		31.1	Euhaline	10.4	78.4	11.2	4.67	2.00	2.67	1.34
EX1	Exe	18-Aug-98	Bar-Built	Macrotidal	MI		20.1	Mesohaline	4.32	44.78	50.9	2.80	2.14	0.66	0.36
EX4	Exe	18-Aug-98	Bar-Built	Macrotidal	MF		28.6	Mesohaline	5.83	67.57	26.6	1.71	2.14	-0.43	-0.24
HW1	Hamford Water	14-Aug-98	Embayment	Mesotidal	SFM		32.1	Euhaline	12.7	81.8	5.5	2.94	2.20	0.74	0.37
HW2	Hamford Water	14-Aug-98	Embayment	Mesotidal	SML	SM6	17.7	Mesohaline	10.5	77.7	11.8	3.40	2.20	1.20	0.60

Appendix 7 continued

Sample	Estuary	Date	Site type	Tidal control	Intertidal habitat	NVC community	Salinity (ppt)	Salinity Category	% Clay	% Silt	% Sand	Redfield ratio (mg C:g)	Total carbon (mg C:g)	Total nitrogen (mg N:g)
HW4	Hamford Water	14-Aug-98	Embayment	Mesotidal	SMM	SM9	23.8	Polyhaline	25.7	63.2	11.1	4.05	2.20	1.85	0.93
HW5	Hamford Water	14-Aug-98	Embayment	Mesotidal	MF		28.7	Polyhaline	10.4	78.7	10.9	1.95	2.20	-0.25	-0.12
HW7	Hamford Water	14-Aug-98	Embayment	Mesotidal	SMB	SM24	24.2	Polyhaline	4.52	47.38	48.1	4.39	2.20	2.19	1.10
HI1	Holy Island	16-Feb-98	Barrier Beach	Macrotidal	SMM	SM13	7.2	Mesohaline	14.8	53.5	31.7	3.98	2.60	1.38	0.63
HI2	Holy Island	16-Feb-98	Barrier Beach	Macrotidal	SMM	SM13	25.2	Mesohaline	4.21	45.09	50.7	3.78	2.60	1.18	0.54
HI3	Holy Island	16-Feb-98	Barrier Beach	Macrotidal	SMM	SM13	43.2	Euhaline	3.83	53.47	42.7	3.71	2.60	1.11	0.51
HI5	Holy Island	16-Feb-98	Barrier Beach	Macrotidal	SML	SM13	18.8	Polyhaline	2.11	27.69	70.2	3.53	2.60	0.93	0.42
HI7	Holy Island	16-Feb-98	Barrier Beach	Macrotidal	SF		11.5	Polyhaline	1.44	13.86	84.7	3.09	2.60	0.49	0.22
BK1	Humber	18/09/98	Coastal Plain	Macrotidal	MF		4.5	Oligohaline	23.3	65.6	11.1	3.80	2.32	1.48	0.44
BK2	Humber	18-Sep-98	Coastal Plain	Macrotidal	MF		5.2	Mesohaline	13.2	77.6	9.2	4.00	2.32	1.68	0.50
BK4	Humber	18-Sep-98	Coastal Plain	Macrotidal	PH	S4	3.3	Oligohaline	8.03	69.17	22.8	5.00	2.32	2.68	0.79
BK5	Humber	18-Sep-98	Coastal Plain	Macrotidal	PH	S4	7.1	Mesohaline	12.5	58.2	29.3	5.70	2.32	3.36	1.00
SM1	Humber	19-Aug-98	Coastal Plain	Macrotidal	SMM	SM14	19.1	Polyhaline	7.5	47.6	44.9	6.85	4.08	2.77	0.86
SM2	Humber	19-Aug-98	Coastal Plain	Macrotidal	SMI	SM6	17.5	Mesohaline	12.9	73.8	13.3	5.80	4.08	1.72	0.53
SM3	Humber	19-Aug-98	Coastal Plain	Macrotidal	PA WET		19.5	Polyhaline	11.3	69.9	18.8	5.88	4.08	1.80	0.56
SM5	Humber	19-Aug-98	Coastal Plain	Macrotidal	MF		16.4	Mesohaline	15	75.3	9.7	3.06	4.08	-1.08	-0.32
SP1	Humber	19-Aug-98	Coastal Plain	Macrotidal	SF		17.0	Mesohaline	0.51	1.63	97.86	0.90	4.08	-3.18	-0.99
SP2	Humber	19-Aug-98	Coastal Plain	Macrotidal	SF		16.7	Mesohaline	0.55	1.75	97.7	2.23	4.08	-1.85	-0.58
SP3	Humber	19-Aug-98	Coastal Plain	Macrotidal	SF		13.9	Mesohaline	0.19	0.31	99.5	3.00	4.08	-1.08	-0.34

Appendix 7 continued

Sample	Estuary	Date	Site type	Tidal regime	NVC	NVC community	Salinity	Salinity Categories	% Clay	% Silt	% Sand	Mean grain size (phi)	Organic matter content (%)	Organic carbon content (%)
WK1	Humber	20-Aug-98	Coastal Plain	Macrotidal	MF		19.9	Polyhaline	6.56	58.64	34.8	4.75	4.08	0.67	0.23
WK2	Humber	20-Aug-98	Coastal Plain	Macrotidal	MF		17.7	Mesohaline	6.29	41.81	51.9	5.35	4.08	1.27	0.43
WK3	Humber	20-Aug-98	Coastal Plain	Macrotidal	PA WET		27.3	Polyhaline	12.1	79.3	8.6	5.82	4.08	1.74	0.60
WK4	Humber	20-Aug-98	Coastal Plain	Macrotidal	MF		21.0	Polyhaline	11.7	80.9	7.4	6.04	4.08	1.96	0.67
WK5	Humber	20-Aug-98	Coastal Plain	Macrotidal	SML	SM6	18.6	Polyhaline	8.1	61.5	30.4	6.08	4.08	2.00	0.68
WK6	Humber	20-Aug-98	Coastal Plain	Macrotidal	SMM	SM14	15.6	Mesohaline	11	76	13	6.49	4.08	2.41	0.83
WK7	Humber	20-Aug-98	Coastal Plain	Macrotidal	SMH	SM13	21.3	Polyhaline	10.7	73.2	16.1	7.00	4.08	2.92	1.00
LY1	Lymington	16-Aug-98	Coastal Plain	Mesotidal	CR		32.8	Euhaline	7.85	75.15	17	2.43	1.97	0.46	0.63
LY3	Lymington	16-Aug-98	Coastal Plain	Mesotidal	SMH	SM14	19.1	Polyhaline	8.55	68.95	22.5	2.30	1.97	0.33	0.46
LY4	Lymington	16-Aug-98	Coastal Plain	Mesotidal	SMH	SM14	26.7	Polyhaline	6.05	59.35	34.6	2.69	1.97	0.72	0.99
LY5	Lymington	16-Aug-98	Coastal Plain	Mesotidal	CR		24.8	Polyhaline	0	0	0	2.19	1.97	0.22	0.30
LY6	Lymington	16-Aug-98	Coastal Plain	Mesotidal	MF		25.5	Polyhaline	7.14	65.56	27.3	1.40	1.97	-0.57	-0.78
MD1	Mawddach	17-Sep-98	Bar-Built	Macrotidal	SF		5.1	Oligohaline	0.97	2.77	96.26	5.06	2.64	2.42	1.02
MD2	Mawddach	17-Sep-98	Bar-Built	Macrotidal	SF		8.3	Mesohaline	2.12	11.78	86.1	2.23	2.64	-0.41	-0.17
MD3	Mawddach	17-Sep-98	Bar-Built	Macrotidal	CR		5.8	Mesohaline	1.19	5.05	93.76	1.84	2.64	-0.80	-0.34
MD6	Mawddach	17-Sep-98	Bar-Built	Macrotidal	SML	SM6	11.9	Mesohaline	10.2	74.2	15.6	3.78	2.64	1.14	0.48
MD7	Mawddach	17-Sep-98	Bar-Built	Macrotidal	SMH	MG11	7.7	Mesohaline	7.69	54.91	37.4	4.49	2.64	1.85	0.78
BH3	North Norfolk Coast	24-Mar-98	Barrier Beach	Mesotidal	PA DRY		17.7	Mesohaline	12.1	78.8	9.1	2.00	0.00	2.00	0.87

Appendix 7 continued

Sample id	Estuary	Date	Site Type	Background Habitat	NVC Community	Salinity (ppt)	Salinity Categories	% Clay	% Silt	% Sand	Weight (mOD)	Depth Hull (mOD)	Thermoclalize to Mud	Thermoclalize to Mud Corrected for Depth
BH5	North Norfolk Coast	24-Mar-98	Barrier Beach	Mesotidal	MF	22.5	Polyhaline	11.8	71.6	16.6	-0.43	0.00	-0.43	-0.19
SK1	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	SF	12.9	Mesohaline	0.89	2.86	96.25	4.47	2.00	2.47	0.67
SK2	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	MF	8.8	Mesohaline	5.13	41.17	53.7	4.39	2.00	2.39	0.64
SK3	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	SML	SM8	18.3	Polyhaline	8.64	66.06	25.3	4.68	2.00	2.68	0.72
SK4	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	SML	SM6	18.5	Polyhaline	10.7	76.8	12.5	4.50	2.00	2.50	0.68
SK6	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	PA DRY		21.5	Polyhaline	8.56	79.44	12	5.09	2.00	3.09	0.83
SK7	North Norfolk Coast	25-Mar-98	Barrier Beach	Mesotidal	SMH	SM13	14.2	Mesohaline	21.2	72.8	6	5.38	2.00	3.38	0.91
PH1	Poole Harbour	17-Aug-98	Bar-Built	Microtidal	PH	S4	15.9	Mesohaline	5.44	45.56	49	2.00	1.50	0.50	0.71
PH2	Poole Harbour	17-Aug-98	Bar-Built	Microtidal	PH	S4	21.2	Mesohaline	7.21	60.59	32.2	1.75	1.50	0.25	0.36
PH3	Poole Harbour	17-Aug-98	Bar-Built	Microtidal	MF		26.6	Mesohaline	7.75	77.55	14.7	1.70	1.50	0.20	0.29
PH4	Poole Harbour	17-Aug-98	Bar-Built	Microtidal	MF		26.8	Mesohaline	7.64	77.16	15.2	1.65	1.50	0.15	0.22
AU3	Severn	23-Apr-98	Coastal Plain	Macrotidal	SML	SM6	6.2	Mesohaline	9.78	77.42	12.8	9.89	6.47	3.42	0.52
AU5	Severn	23-Apr-98	Coastal Plain	Macrotidal	MF		8.6	Mesohaline	12.3	80.3	7.4	5.66	6.47	-0.81	-0.12
AU6	Severn	23-Apr-98	Coastal Plain	Macrotidal	SMM	SM13	2.1	Oligohaline	11.2	79.1	9.7	13.00	6.47	6.53	1.00
BH2	Severn	25-Apr-98	Embayment	Macrotidal	SMM	SM13	4.2	Oligohaline	11.9	73.5	14.6	10.79	6.00	4.79	0.96

Appendix 7 continued

SampleId	Estuary	Date	Site type	Tidal regime	Habitat	IVC community	Salinity g/l	Salinity Categories	% Clay	% Silt	% Sand	Height (mOD)	Depth of ML (mOD)	Height relative to MT	Normalised tidal height
BB3	Severn	25-Apr-98	Embayment	Macrotidal	SML	SM6	5.4	Mesohaline	12.1	74.3	13.6	10.52	6.00	4.52	0.90
BB5	Severn	25-Apr-98	Embayment	Macrotidal	SF		13.7	Mesohaline	0.54	1.36	98.1	9.22	6.00	3.22	0.64
BB6	Severn	25-Apr-98	Embayment	Macrotidal	MF		14.8	Mesohaline	12.1	77.2	10.7	7.45	6.00	1.45	0.29
BB7	Severn	25-Apr-98	Embayment	Macrotidal	PH	S4	2.8	Oligohaline	15.1	71.1	13.8	11.08	6.00	5.08	1.02
WL1	Severn	24-Apr-98	Coastal Plain	Macrotidal	MF		12.4	Mesohaline	16.1	81.8	2.1	7.21	6.17	1.04	0.17
WL2	Severn	24-Apr-98	Coastal Plain	Macrotidal	MF		9.8	Mesohaline	15.4	80.6	4	9.31	6.17	3.14	0.53
WL3	Severn	24-Apr-98	Coastal Plain	Macrotidal	MF		7.1	Mesohaline	12.5	77.4	10.1	9.73	6.17	3.56	0.60
WL5	Severn	24-Apr-98	Coastal Plain	Macrotidal	SMH	SM13	2.7	Oligohaline	9.96	69.84	20.2	12.02	6.17	5.85	0.99
WL6	Severn	24-Apr-98	Coastal Plain	Macrotidal	SMH	SM27	9.5	Mesohaline	10.9	73.6	15.5	11.91	6.17	5.74	0.97
WL7	Severn	24-Apr-98	Coastal Plain	Macrotidal	MF		14.1	Mesohaline	13.3	79.4	7.3	6.20	6.17	0.03	0.01
BS1	Solway Firth	18-May-98	Complex	Macrotidal	SMH	SM16	3.7	Oligohaline	2.11	29.49	68.4	7.10	3.21	3.89	1.00
BS2	Solway Firth	18-May-98	Complex	Macrotidal	PA WET		27.1	Polyhaline	3.58	45.72	50.7	6.07	3.21	2.86	0.74
BS3	Solway Firth	18-May-98	Complex	Macrotidal	SMH	SM16	10.8	Mesohaline	2.58	33.72	63.7	6.55	3.21	3.34	0.86
BS5	Solway Firth	18-May-98	Complex	Macrotidal	SFM		13.0	Mesohaline	1.5	9.4	89.1	4.65	3.21	1.44	0.37
BS6	Solway Firth	18-May-98	Complex	Macrotidal	SF		15.4	Mesohaline	1.31	5.73	92.96	1.83	3.21	-1.38	-0.36
CK1	Solway Firth	19-May-98	Complex	Macrotidal	SF		16.3	Mesohaline	2.07	18.73	79.2	5.43	3.21	2.22	0.57
CK3	Solway Firth	19-May-98	Complex	Macrotidal	SFM	SM8	33.3	Euhaline	4.07	56.63	39.3	5.92	3.21	2.71	0.70
CK4	Solway Firth	19-May-98	Complex	Macrotidal	PA WET		18.4	Polyhaline	3.48	50.52	46	6.73	3.21	3.52	0.91
CK5	Solway Firth	19-May-98	Complex	Macrotidal	SMH	SM16	4.7	Oligohaline	3.66	50.64	45.7	7.10	3.21	3.89	1.00

Appendix 7 continued

Sample	Estuary	Date	Site type	Tidal regime	Intertidal habitat	MNCR community	Salinity (ppt)	Salinity Category	Redox (mV)	%Silt	%Sand	%Gravel (mz Phi)	Depth (m)	Depth below MSL (m)	Normalised depth (z)
CK6	Solway Firth	19-May-98	Complex	Macrotidal	SMB	SM28	0.9	Oligohaline	7.08	39.72	53.2	7.59	3.21	4.32	1.12
SB1	Solway Firth	20-May-98	Fjard	Macrotidal	MF		22.2	Polyhaline	7.54	78.76	13.7	6.37	3.73	2.94	0.81
SB3	Solway Firth	20-May-98	Fjard	Macrotidal	SFM		21.8	Polyhaline	4.96	65.14	29.9	5.45	3.73	1.72	0.53
SB4	Solway Firth	20-May-98	Fjard	Macrotidal	SF		15.3	Mesohaline	1.42	8.98	89.6	5.32	3.73	1.59	0.45
SB5	Solway Firth	20-May-98	Fjard	Macrotidal	SF		14.2	Mesohaline	3.89	47.71	48.4	4.64	3.73	0.91	0.28
WT1	Solway Firth	21-May-98	Fjard	Macrotidal	SFM		27.3	Polyhaline	4.06	50.84	45.1	5.38	3.73	1.65	0.50
WT3	Solway Firth	21-May-98	Fjard	Macrotidal	SML	SM11	24.1	Polyhaline	4.66	61.34	34	6.13	3.73	2.40	0.73
WT5	Solway Firth	21-May-98	Fjard	Macrotidal	SMH	SM15	7.0	Mesohaline	5.84	56.06	38.1	6.90	3.73	3.17	0.97
WT6	Solway Firth	21-May-98	Fjard	Macrotidal	SMB	SM28	3.5	Oligohaline	13.8	59.4	18.8	7.36	3.73	3.63	1.11
HW6	South Coast	14-Aug-98	Embayment	Mesotidal	MF		38.7	Euhaline	10.6	79.8	9.6	1.87	2.20	-0.33	-0.17
FR1	Wash	27-Mar-98	Embayment	Macrotidal	MF		15.5	Mesohaline	9.49	68.81	21.7	5.31	3.85	1.46	0.40
FR3	Wash	27-Mar-98	Embayment	Macrotidal	SML	SM8	13.3	Mesohaline	9.52	71.18	19.3	5.26	3.85	1.41	0.39
FR4	Wash	27-Mar-98	Embayment	Macrotidal	SML	SM14	8.5	Mesohaline	7.75	57.65	34.6	6.47	3.85	2.62	0.72
FR5	Wash	27-Mar-98	Embayment	Macrotidal	SMM	SM10	14.2	Mesohaline	9.37	69.83	20.8	6.51	3.85	2.66	0.73
FR6	Wash	27-Mar-98	Embayment	Macrotidal	SMH	SM13	7.0	Mesohaline	10.6	70.8	18.6	6.35	3.85	2.50	0.69
GP1	Wash	29-Mar-98	Embayment	Macrotidal	SMH	SM13	15.3	Mesohaline	10.0	73.4	16	6.88	4.01	2.87	0.80
GP2	Wash	29-Mar-98	Embayment	Macrotidal	CR		15.4	Mesohaline	9.47	68.53	22	6.27	4.01	2.26	0.76
GP3	Wash	29-Mar-98	Embayment	Macrotidal	SMH	SM14	10.4	Mesohaline	9.62	69.38	21	6.86	4.01	2.85	0.99
GP4	Wash	29-Mar-98	Embayment	Macrotidal	SMB		15.0	Mesohaline	7.47	66.03	26.5	5.79	4.01	1.78	0.62

Appendix 7 continued

Sample Id	Estuary	Date	Site Type	Tidal regime	Habitat	MVC community	Salinity (‰)	Salinity Categories	% Clay	% Silt	% Sand	Weight (mg)	Mean Log2 Weight	Sorted Log2 Weight	Normalised Log2 Weight
SH1	Wash	28-Mar-98	Embayment	Macrotidal	SMH	SM14	9.7	Mesohaline	10.4	66.7	22.9	6.63	3.31	3.5	1.01
SH2	Wash	28-Mar-98	Embayment	Macrotidal	SMM	SM13	9.9	Mesohaline	7.38	54.72	37.9	6.68	3.31	3.37	0.97
SH3	Wash	28-Mar-98	Embayment	Macrotidal	PA WFT		17.3	Mesohaline	11.8	75.6	12.6	6.40	3.31	3.09	0.89
SH4	Wash	28-Mar-98	Embayment	Macrotidal	SML	SM13	13.5	Mesohaline	10.2	72.4	17.4	6.28	3.31	2.97	0.85
SH5	Wash	28-Mar-98	Embayment	Macrotidal	SML	SM8	13.0	Mesohaline	9.24	66.16	24.6	5.95	3.31	2.64	0.76
SH6	Wash	28-Mar-98	Embayment	Macrotidal	CR		15.2	Mesohaline	4.4	26.7	68.9	5.04	3.31	1.73	0.50
SH7	Wash	28-Mar-98	Embayment	Macrotidal	SML	SM8	13.1	Mesohaline	5.72	53.38	40.9	5.71	3.31	2.40	0.69
SH8	Wash	28-Mar-98	Embayment	Macrotidal	SHM		14.0	Mesohaline	1.85	5.41	92.74	5.29	3.31	1.98	0.57

APPENDIX 8

Morphological Properties of Unidentified Taxa

Taxon Name	Description
Achnanthes sp. B	Small linear elliptic valve with broadly rounded apices. Length 7 µm, breadth, 3.5 – 4 µm. Only RLV vale found: striae weakly radiate throughout, around 20/10 µm, axial area a narrow ellipse, broad, up to one third of the value width at the centre.
Biremis sp. A	Valve elliptical with slightly pointed apices, length 15 µm, breadth 5 µm. Raphe straight, axial area a very narrow ellipse, central area small and round. Striae heavy, parallel, 9/10 µm.
Caloneis sp. A	Valve elongated linear-elliptic, length 32 – 42 µm, breadth 7 – 9 µm. Striae punctate, radial at centre to weakly convergent at apices, 16/10 µm. Axial area narrow broadening to a rhombic central area with some irregular, short striae at centre.
Cocconeis sp. A	Small oval valve, length 10 µm, breadth 6 µm. Striae distinctly punctate, each puntae clearly separate. Striae radial throughout, 14/10 µm. Only RLV identified, similarities to smaller RLV of *Cocconeis scutellum* var. *parva*.
Cocconeis sp. C	Small linear-elliptic valve, length 9.5 µm, breadth 4.5 µm. Only RLV found: striae finely punctate, radial throughout, 21/10 µm, axial area narrow throughout.
Gomphonema sp. A	Small, heteropolar, clavate valve, slightly produced weakly capitate foot, rounded head, length 12 µm, breadth 2.5 – 3 µm. Striae close to parallel at centre sometime becoming weakly convergent at poles, around 18/10 µm. Axial area narrow throughout, raphe straight, terminal endings irresolvable in LM. No stigmata visible.
Grammatophora sp. A	Valve linear with broadly rounded to slightly pointed apices, length 7.5 µm, breadth 2.5 µm. Two psuedosepta on valve surface, straight, perpendicular to the linear sides across full width of the valve, approximately splits the valve into thirds. Finer features of the valve not resolvable in LM.
Navicula sp. A	Small linear lanceolate valve with broadly rounded apices, length 12-13 µm, breadth 3 µm. Striae distinct but fine, 20-22/20 µm, radiate throughout but more strongly at centre. Axial area narrow, central area indistinct or absent. Similarities with the finer, smaller end of Navicula salinicola, could also be an *Achnanthes* sp.
Navicula sp. B	Value linear-elliptic with rounded ends, length 20-22 µm, breadth 5.5 – 6 µm. Striae the most distinctive feature being weakly radiate throughout but more strongly radial at the centre on one side of the valve only where there are curves striae and one shorter one just off centre, 16-18/10 µm. Axial area narrow broadening to a very narrow, apically elongated, ellipse towards the centre of the valve. Central area rhombic and asymmetrical due to the difference in striae either side of the central raphe endings. Raphe straight terminal endings deflected in same direction, weakly inflated at central endings, which are close. Valve shape very similar to *Navicula cincta* but striae density and pattern do not fit any species of a subsp. description.
Navicula sp. C	Valve shape similar to Navicula sp. B but with more pointed apices, very weakly produced. Length 18 µm, breadth 4.5 µm. Striae distinct, parallel throughout to very weakly radial at centre, 16/10 µm. Raphe straight, axial area narrow at apices abrupt widening to a narrow apically elongate rectangle for half the length of the valve over the centre.
Nitzschia sp. A	Valves linear with weakly concave dorsal margin, apices capitate and curved towards ventral side, length 21 µm, breadth 4 µm. Fibulae on ventral margin, 12/10 µm, striae indistinct, around 24/10 µm. Raphe very close to ventral margin, Resemblance to *Nitzschia morosa* (Cholnoky).
Opephora sp. A	Very small valve, heteropolar ellipse with broadly rounded apices, length 4-6 µm, breadth 1.5-2.5 µm. Striae short, distinct, roughly parallel and alternate, 10-14/10 µm. Possibly a small form of a common coastal *Opephora* species such as *Opephora olsenii* or *parva* but measurements incorrect for the smaller end of either species' morphological range.

Appendix 8 continued

Taxon Name	Description
Thalassiosira sp. A	Small valve, D 7 µm. Areolae in parallel rows, although not as strictly as, e.g. *Thalassiosira tenera*, larger at centre, on average 18/10 µm. 5 marginal processes.
Thalassiosira sp. B	Valve D 18 µm. Areolae around 13-15/10 µm, arranged in an untidy star shape from centre. Appears to be a central process but exact morphology at centre of valve not resolvable in LM. 4-5 marginal processes/10 µm. Similarities with *Thalassiosira pacifica* and *wongii*.
Unknown sp. A	Valves linear elliptic with rostrate apices, length 32 µm, breadth 7.5 µm. Striae distinct, parallel, weakly radial at centre, weakly convergent at poles, 11/10 µm. Raphe straight, terminal endings indistinct, axial area very narrow, central area small ellipse elongates apically. In specimen recorded the valve is broader one side of the raphe, this could suggest a *Cymbella* sp., or a Naviculoid sp., lying partly on its side.